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The Postcranial Skeleton of African Cynodonts

Farish A. Jenkins, Jr.

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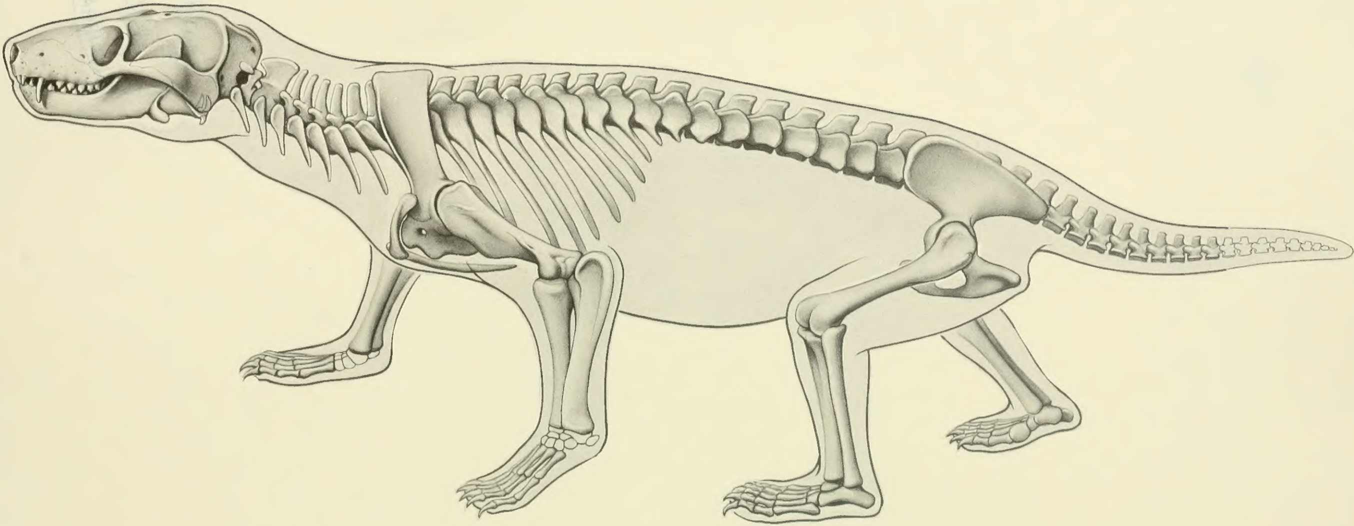

Skeletal reconstruction of the cynodont *Thrinaxodon liorhinus,* approximately X1/2. This reconstruction is based primarily on the following specimens: axial skeleton, AMMM 5265; appendicular skeleton, SAM 1395; skull, USNM 22812 and other specimens (uncatalogued) belonging to the South African Museum.

The Postcranial Skeleton of African Cynodonts

Problems in the Early Evolution of the Mammalian Postcranial Skeleton

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THE POSTCRANIAL SKELETON OF AFRICAN CYNODONTS

Problems in the Early Evolution of the Mammalian Postcranial Skeleton

By Farish A. Jenkins, Jr.

ABSTRACT

Cynodonts are advanced mammal-like reptiles from which mammals probably were derived during Middle or Late Triassic times. The cynodont-mammal relationship, originally postulated primarily on the basis of cranial morphology, is here re-examined on evidence from postcranial anatomy. This study describes the postcranial skeleton of African cynodonts and offers functional interpretations with particular emphasis on posture and locomotion. *Cynognathus*, *Diademodon*, *Galesaurus* and *Thrinaxodon* are the principal genera studied; these and other cynodonts appear to have been very similar in their postcranial anatomy.

The cynodont atlas-axis complex, although basically reptilian in pattern, is incipiently specialized to permit atlanto-occipital flexion and extension as well as atlanto-axial rotation. Differentiation of the dens from the atlas centrum began in cynodonts and represents a functional replacement of the atlanto-axial zygapophyses lost to permit atlanto-axial rotation. The dens is not the homologue of the atlas centrum as is usually claimed on embryological evidence but is a neomorphic process of the atlas centrum.

During locomotion, the cynodont axial skeleton probably did not flex and extend in the sagittal plane as in mammals. Lateral undulation, typical of axial movement in reptiles, may have been facilitated in cynodonts by an enlarged iliocostalis system of muscles inserting on the costal plates. Functionally, the imbricating costal plates may be analogous to the expanded ribs in certain edentates and may represent part of a musculoskeletal adaptation to sustain a more characteristically "mammalian" posture with the trunk held persistently off the ground.

The cynodont glenoid was oriented posterolaterally and somewhat ventrally. The long axis of the humerus approximated a 45° angle to a parasagittal plane. Much of the propulsive force was transmitted directly to the scapula as in mammals. Propulsive movements of the humerus involved a significant amount of elevation and depression, thus presaging the movement typical of mammals. It is likely that some long axis rotation of the humerus, a primitive characteristic, was retained.

Like the forelimb and shoulder girdle, the cynodont hindlimb and pelvis possess a number of postural and morphological features that are advanced toward a mammalian condition. Among these are an obturator foramen of mammalian proportions, a socket-like acetabulum, and a bulbous, inflected humeral head. The femur was held at angles of about 55° to a parasagittal plane. The mammalian lesser trochanter was derived from the reptilian trochanter internus by a slight shift in muscular insertion related to the repositioning of the limbs. In the cynodont foot a well-developed tuber calcis, sustentaculum tali, transverse tarsal arch and complex tarso-intermetatarsal articulations are all mammalian features. The pes, in one genus at least, was plantigrade and like the manus had the mammalian phalangeal formula of 2-3-3-3-3.

In details of morphology and function the postcranial skeleton of cynodonts should be regarded as neither "reptilian" nor "mammalian" but as transitional between the two classes. It is inappropriate to conceive of monotremes as representing a prototherian level of organization for in many ways monotremes are highly specialized.

ZUSAMMENFASSUNG

Die Cynodontier sind fortgeschrittene, den Säugetieren ähnliche Reptile, von welchen die Säugetiere wahrscheinlich während der mittleren oder späteren triassischen Zeit abstammten. Der Zusammenhang zwischen Cynodontier und Säugetieren, welcher ursprünglich hauptsächlich auf Grund der kranialen Morphologie postuliert wurde, wird hier erneut durch Befunde an der post-kranialen Anatomie untersucht. Diese Arbeit beschreibt das post-kraniale Skelett afrikanischer Cynodontier und bietet funktionsbedingte Auslegungen in welchen Haltung und Fortbewegen besonders berücksichtigt werden. *Cynognathus*, *Diademodon*, *Galesaurus* und *Thrinaxodon* sind die prinzipiellen Genera welche studiert wurden; diese und andere Cynodontier scheinen, in Bezug auf ihre post-kraniale Anatomie, sehr ähnlich gewesen zu sein.

Der Cynodontier Atlas-Achse Komplex, obwohl durchaus Reptile artig, zeigt eine anfängliche Spezialisierung um atlanto-occipitales Beugen und Strecken sowie atlanto-axiales Drehen zu erlauben. Die Differenzierung des Dens vom Atlas Zentrum begann in den Cynodontier und stellt einen funktionsbedingten Ersatz dar, für die atlanto-axiale Zygapophyse welche verloren war um eine atlanto-axiale Drehung zu ermöglichen. Der Dens ist kein Homolog des Atlas Zentrums als gewöhnlich behauptet auf Grund embryologischer Befunde, sondern ein neomorphischer Knochenfortsatz des Atlas Zentrums.

Im Fortbewegen hat das axiale Skelett der Cynodontier sich wahrscheinlich weder gebeugt noch gestreckt in einer sagittalen Ebene wie das der Säugetiere. Seitliche wellenförmige Bewegungen, die typische axiale Bewegungsweise der Reptile, könnten in Cynodontier erleichtert gewesen sein durch ein erweitertes ilio-costalisches Muskel System welches in den erweiterten Rippen eingeschoben war. Diese übereinanderliegenden erweiterten Rippen können den ausgedehnten Rippen mancher Edentaten entsprochen haben und eine muskulo-skelettale Anpassung vorstellen um eine mehr "Säugetier-artige" Stellung zu erhalten in welcher der Rumpf beharrlich oberhalb der Erde gehalten wurde.

Die Gelenkgrube des Schultergürtels der Cynodontier war posterolateral und etwas ventral orientiert. Der Winkel der langen Humerus-Achse betrug ungefähr 45 Grade zu einer parasagittalen Ebene. Ein grosser Teil der vorwärts treibenden Kraft wurde

wie in den Säugetieren direkt zur Scapula übertragen. Fortbewegungen des Humerus benötigten bedeutendes Erheben und Senken, in welchen die typischen Säugetier Bewegungen vorbedeutet sind. Wahrscheinlich wurde eine lange Achsendrehung des Humerus, ein primitiver Charakterzug, beibehalten.

Wie das Vorderbein und der Schultergürtel so besassen auch das Hinterbein und das Becken der Cynodontier einige morphologische Bildungen und eine körperliche Haltung die eine Annäherung an die Säugetiere zeigen. Das Obturator foramen hatte das Ausmass der Säugetiere, das Acetabulum war höhlenartig und der knollenartige Kopf hatte eine etwas seitlich gedrehte Haltung. Das Femur wurde in 55 gradigem Winkel zu einer parasigittalen Ebene gehalten. Das Trochanter minor der Säugetiere entstand vom Trochanter internus der Reptile durch eine geringe Veränderung einer Muskel Insertion im Zusammenhang mit der geänderten Stellung der Extremitäten. Zu diesen Zügen der Säugetiere zählen ein gut entwickeltes Tuber calcis, ein Sustentaculum tali, eine transverse tarsale Wölbung und komplizierte tarso-intermetatarsale Gliederungen im Fusse der Cynodontier. Zumindest eine Gattung hatte einen plantigraden Fuss, der, wie die Hand, die Phalangenformel von 2-3-3-3-3 der Säugetiere besass.

In den Details der Morphologie und Funktion sollte das post-kraniale Skelett der Cynodontier weder as "Reptile" noch als "Säugetier" artig betrachtet werden, sondern als ein Ubergang zwischen beiden Arten. Es ist nicht angebracht Monotremen als ein Exemplar einer Vorstuffe der Säugetiere anzusehen, da die Monotremen in vielen Beziehungen spezielle Bildungen besitzen.

РЕЗЮМЕ

К вопросу о заднечеренном скелете африканских цинодонтов и проблемы ранней эволюции заднечерепной анатомии млекопитающих

Цинодонты являются высокоразвитыми млекопитающеподобными пресмыкающимися к которым вероятно восходят млекопитающие. Это приурочивается к среднему и верхнему триасу. Взаимоотношение между цинодонтами и млекопитающими первоначально постулируется в первую очередь на основании черепной морфологии, пересматривается в настоящей работе с применением данных заднечерепной анатомии. В этом исследовании описывается заднечерепной скелет африканских цинодонтов и предлагаются функциональные истолкования, особенно подчёркивая положения тела и передвижение. Основными исследуемыми родами являются: *Cynognathus*, *Diademodon*, *Galesaurus*, *Thrinaxodon*. У этих цинодонтов, как и у других, выявляются существенные сходства по заднечерепной анатомии.

Хотя атлантоаксиальный комплекс цинодонтов в основных своих чертах соответствует модели пресмыкающихся, но является зачаточно-специализированным, чтобы позволить атланто-затылочное сгибание и растягивание как и атлантоаксиальное вращение. Дифференциация между зубовидным отростком и телом атлантового позвонка возникла первоначально у цинодонтов и представляет функциональное замещение атлантоаксиального сочленовного отростка в результате исчезновения которого стало возможным атлантоаксиальное вращение. Зубовидный отросток не является гомологом тела атлантового позвонка как обычно утверждают на основании эмбриологических данных, а являются его неоморфным процессом.

Во время передвижения, аксиальный скелет цинодонта вероятно не сгибался и не растягивался в сагиттальной плоскости подобно млекопитающим. Возможно что боковой ундулеции, которой характеризуется аксиальное движение пресмыкающихся, способствовала у цинодонтов увеличенная подвздошно-реберная мышечная система прикрепляющаяся к реберным пластинкам. С функциональной точки зрения, возможно что черептчаторасположенные реберные пластинки аналогичны расширенным ребрам у определенных эдентатов и представляют часть скелетно-мышечной адаптации целью которой является более характерная "млекопитающим" способ держать тело с постоянно приподнятым туловищем.

Суставная впадина лопатки у цинодонтов была постеролатерально и до некоторой степени вентрально направлена. Угол продольной оси плечевой кости к парасагиттальной плоскости равнялся приблизительно 15 градусам. Значительная часть пропульсивной силы передавалась прямо на лопатки, подобно млекопитающим. Пропульсивные движения плечевой кости сопровождали значительное суммарное движение вверх и вниз, таким образом предвещая движения характеризующие млекопитающих. По всей вероятности сохранилось определенное вращение продольной оси плечевой кости, являющееся примитивной чертой.

Как передние конечности и плечевой пояс, так и задние конечности и таз у цинодонтов обладают несколькими свойствами относящимися к морфологии и к способу держать тело, развивавшимися в направлении к млекопитающим. Среди этих черт следует отметить запирательное отверстие соответстующее пропорциям у млекопитающих, впадиноподобное *acetabulum*, луковицеобразная, вогнутая плечевая головка. Бедро держалось приблизительно под углом 55 градусов к парасагиттальной плоскости. Малый вертлюг у млекопитающих восходит к рептильному внутреннему вертлюгу, с небольшим смещением мышечного прикрепления относящегося к переставлению конечностей. Стопа ноги у цинодонта характеризуется следующими чертами млекопитающих: хорошо развитый бугор пяточной кости, поддерживающий надпяточную кость; поперечная предплюсневая дуга; и комплексные предплюснемежплюсневые суставы. Нога, по крайней мере у одного рода, была стопоходящей и подобно руке имела суставную формулу пальцев млекопитающих (2-3-3-3-3).

Что касается подробностей морфологии и функции, заднечерепной скелет у цинодонтов не следует считать ни "рептильным", ни относящимся к "млекопитающим", а переходным между двумя классами. Неуместно предполагать, что цинодонты достигли уровня организации соответствующего яйцекладущим млекопитающим, ибо во многих отношениях однопроходные являются высокоспециализированными животными.

INTRODUCTION

The evolutionary emergence of the Class Mammalia involved a period of transition some 100 million years long. During this time, mammalian forebears gradually acquired much of the basic structure which now characterizes living members of the class. But the transition between the earliest synapsids and the earliest therians is represented by an obviously incomplete fossil record. Despite its incompleteness, however, a great diversity of transitional forms is known. Cynodonts represent one of the most advanced groups of reptiles which manifest many mammal-like features. In the cynodont skull, for example, features which represent or otherwise anticipate the mammalian pattern are the double occipital condyles, the secondary palate, the ethmoturbinals and the proportionately large dentary bone. African cynodonts were small to medium-sized animals, varying in length from approximately 35 cm (*Thrinaxodon*) to as much as 150 cm or more (*Cynognathus*). The cynodont dentition underwent rapid evolutionary change, partly the result of dietary specialization but also in conjunction with musculoskeletal changes in the lower jaw. Traversodontids and diademodontids undoubtedly were herbivorous; procynosuchids and galesaurids were probably insectivorous and carnivorous, while most cynognathids were strictly carnivorous. The taxonomic interrelationships of cynodonts and related forms constitutes a significant problem in itself, and complicates the search for the origin of mammalian anatomical features. In this study no attempt is made to solve questions as to the origin or interrelations of cynodonts, the solution to which must come from studies on cranial morphology (see Watson and Romer, 1956; Romer, 1969b).

The scope of the present survey is restricted to African cynodonts. Earlier research on South American cynodonts (von Huene, 1935-1942; 1944-1948; Cabrera, 1943) is now being supplemented and expanded by Bonaparte (1962–1966e and later papers) and Romer (1966, 1969a, 1969b). I have recently described the postcranial skeleton of a new traversodontid from Argentina (Jenkins, 1970a) but aside from this study have not had the opportunity to examine other South American material. For this reason I make only limited reference to South American cynodonts and base my conclusions primarily on the excellent papers of Bonaparte. Of the Russian forms, only a description of the postcranial skeleton of *Permocynodon* (Konjukova, 1946) is available.

The present study on the postcranial skeleton of African cynodonts has a dual purpose: first, to provide an adequate morphological basis for comparison with postcrania in other therapsids and in early mammals, and second, to evaluate the cynodont postcranial skeleton as a possible stage in the evolution of mammalian features.

No comparative survey of the cynodont postcranial skeleton has even been published nor has the role of cynodonts in the evolution of mammals been universally acknowledged. Both of these facts are best understood in their historical context which now will be briefly summarized.

In 1844, Sir Richard Owen described the first mammal-like reptile (*Dicynodon*) from cranial material collected by A. G. Bain some years earlier. Owen compared the cranial features of this fossil to various orders of reptiles, concluding that "the general type of cranial organization manifested by modern lizards was that in which the peculiar modifications of the *Dicynodon* have been superinduced." Only the long tusks gave Owen any reason to make reference to mammals. Citing seemingly appropriate analogies with mammalian tusks and canine teeth, he added that *Dicynodon* manifested a "much more important step towards the mammalian type of dentition by maintaining the serviceable state of the tusk by virtue of constant renovation . . . according to the principle manifested in the long-lived and ever-growing tusks and scalpriform incisors of the Mammalia." This was, for Owen, the only implication of mammalian affinities of *Dicynodon*, and obviously he regarded it as a peculiarity of no phylogenetic importance.

For the three decades following Owen's original description, papers by Owen and others on mammal-like reptiles were devoted primarily to describing morphological aspects of the cranium, with little attention paid to the postcranial skeleton. In general, these papers disclosed a general lack of appreciation of the mammal-like features and affinities of therapsids. Within the context of mid-nineteenth century paleontology, it is even surprising that the evolutionary status of Karroo fossils was recognized as soon as it was. As early as 1861 Owen wrote that *Galesaurus planiceps* possesses "that remarkable resemblance to the mammalian carnivorous dentition, which has led to a foundation of a family [Cynodontia] for its reception in the group of reptiles characterized by the anomalous departures from the type of dentition in the great Saurian order of Cuvier." Yet the many reptilian features of these fossils, and the fact that Huxley and others maintained that mammals arose directly from Amphibia, delayed recognition that therapsids were the stock from which mammals arose.

Owen's monographic *Catalogue of the Fossil Reptilia of South Africa* (1876) contains several allusions to the mammal-like features of theriodonts and anomodonts. Most of the comparisons, however, were made with dinosaurs and living reptiles. Evidently Owen could not bring himself to accept the possibility that among them were the reptilian ancestors of mammals. Of the mammal-like features of anomodonts and theriodonts he concluded: "Certain it is that the lost reptilian structures specified in the present Catalogue are now manifested by quadrupeds with a higher condition of cerebral, circulatory, respiratory and tegumentary systems [i.e., mammals] —a condition the acquisition of which is unintelligible to the writer on either the Lamarckian or Darwinian hypothesis."

In November, 1878, E. D. Cope read a paper before the National Academy of Sciences in which he proposed the Pelycosauria and Anomodontia (including all South African therapsids then known) as Suborders of the Order Theromorpha. This order he "regarded . . . as approximating the Mammalia more closely than any other division of Reptilia, and as probably the ancestral group from which the latter were derived" (Cope, 1878: 829 830). The misuse of the word "latter" muddles Cope's intended meaning. Cope's remarks were transcribed and probably not reviewed by him prior to the issue of the *Proceedings*. In any event, it is clear from the context that Cope proposed that mammals, not reptiles, arose from the Theromorpha. This marks one of the earliest positive statements on the reptilian ancestry of mammals. Owen speculated along similar lines in 1880, suggesting that monotremes might be derived from Karroo Triassic reptiles.

Paleontologists of the last two decades of the nineteenth century were fully occupied with descriptive studies of an abundance and diversity of Permo-Triassic vertebrates. A minor polemic over a suitable classification occupied Cope and H. G. Seeley; both of these authors, although cognizant of the pre-mammalian status of therapsids, did little to advance the investigation of mammal origins. In 1888 Seeley concluded, with reference to *Pareiasaurus* and allied genera, that their "mammalian structures have been transmitted to mammals, if not in direct line, which is improbable, by collateral derivation from a common ancestry." Ten years later, at a meeting of the International Congress of Zoology, the origin of mammals was discussed by Seeley, H. F. Osborn, O. C. Marsh, Haeckel and others (Seeley, et al., 1898: 69–76). Seeley acknowledged that theriodonts could be regarded as mammalian ancestors, but cited so much apparently conflicting evidence that the matter could not be conclusively settled. He concluded that "anomodonts [which to Seeley meant anomodonts *sensu stricto* plus theriodonts] are not the ancestors of mammals, but a collateral and closely related group. The common parent of both may be sought in rocks older than the Permian, perhaps in Silurian and Devonian strata." Osborn agreed with Seeley's view that no known therapsid could be a mammalian ancestor. But he suggested, instead, that a then unknown group of "anomodonts" (*sensu latu*) gave rise to mammals, and that many mammalian characters shared by known "anomodonts" and mammals were the result of independent, parallel acquisition. Marsh cited the fact that known mammals were so diverse as to leave "an open question whether all have a common origin"—thereby introducing the question of polyphyly. Marsh favored the Huxleyian theory of mammalian derivation directly from amphibians. Thus, at the turn of the century, the question of the origin of mammals was largely unresolved.

The development of viable theories of mammalian origins, as well as the understanding of relationships within the Therapsida, is largely the work of Robert Broom and D. M. S. Watson. As early as 1901, Broom hypothesized that mammals arose from primitive theriodonts, on or near the stem which gave rise to *Cynognathus* and *Diademodon*. In 1905, he specifically included cynodonts in the mammalian lineage, and repeated this opinion (Broom, 1907, 1913a, 1915) as better material became known. At about the same time Watson (1913) thought that a "pre-therocephalian" was the common ancestor of therocephalians, cynodonts and mammals. Shortly thereafter he changed his opinion, stating that the Suborder Gorgonopsia gave rise to mammals (Watson, 1917b). The discovery of ictidosaurs re-emphasized the mammal-like characters of cynodonts and Broom advocated that mammals were derived from ictidosaurs and these, in turn, arose from cynodonts (Broom, 1929). Later, Broom (1932b) reaffirmed his opinion that mammals originated from ictidosaurs but expressed uncertainty over ictidosaur origins, inclining to the belief that ictidosaurs evolved from "a small primitive Bauriamorph" rather than "a small primitive cynodont".

Despite Broom's last and somewhat equivocal opinion on cynodont-ictidosaur relationships, there is little doubt that the cynodont skull possesses numerous mammalian features (as demonstrated by Broom, Watson, Brink and others). Recent work has brought forward additional evidence for a cynodont-mammal relationship (see Hopson and Crompton, 1969). Brink (1967), however, still prefers the alternate hypothesis that mammals arose from a bauriamorph (*sensu* Watson and Romer, 1956) although this relationship is not supported by any recent morphological analysis. The hypothesis of a bauriamorph-mammal relationship probably derives from Broom's (1909) original description of *Bauria* as a primitive cynodont rather than as a representative of a new infraorder, the Bauriamorpha. For some time, at least, Broom (1929: 690) "was inclined to find the mammalian ancestor in one of the Bauriamorphs". But aside from a few incidental references to the secondary palate and other advanced features, no worker has since been able to establish that bauriamorphs are more likely to have been mammalian ancestors than cynodonts. Yet the hypothesis persists. For example, Crompton (1955a, 1958) concluded that the ictidosaur *Diarthrognathus* could not have been derived from any known cynodont and suggested that it was derived from bauriamorphs. Thus Brink (1956), following Crompton, diagrammatically represented the line of mammalian evolution passing from *Scaloposaurus*, close to *Bauria*, through the ictidosaurs to mammals. However, Kermack (1967) and Crompton (*in* Crompton and Jenkins, 1968) now believe that ictidosaurs represent advanced but somewhat aberrant cynodonts and have no part in mammalian ancestry (a view expressed by von Huene in 1940). Thus the theory of a bauriamorph origin for mammals as advocated by Brink appears to be even less tenable. At the present time Triassic mammals are becoming better known and cynodonts are favored as percursors of some, if not all, of Triassic groups of mammals on the basis of cranial structure and dentition (Hopson, 1964, 1967; Crompton and Jenkins, 1968; Hopson and Crompton, 1969).

The history of studies on cynodont postcrania is short. Owen (1876: 21, Pl. XIX) briefly described the coracoids and parts of a left humerus of *Cynochampsa laniarius* (considered questionably synonymous with *Diademodon* by Watson and Romer, 1956: 65). This material, which could not be located for re-examination, probably represents a cynodont and was thus the first cynodont postcranial remains to be described. Subsequent to Seeley's (1895a, 1895b) monographs on *Cynognathus* and other genera, descriptions of cynodont postcranial material were usually incidental to discussions of cranial morphology. Broom, Broili and Schröder, Crompton, Haughton, Parrington, von Huene and Watson all described various aspects of incomplete and sometimes generically indeterminate postcrania. More recently, Brink and Kitching have published the most comprehensive accounts of African cynodont postcrania since Seeley's papers.

Without detracting from the contributions of the aforementioned authors, it should be noted that the available cynodont material was and still is, in quantity and quality, much less than might be desired for so important a group. To some extent the present study suffers from these inadequacies. However, this disadvantage is partially offset by new material as well as by the fact that the major differences between cynodont genera are in cranial morphology. The postcranial skeletons, insofar as known, are remarkably alike. Thus it is possible to present a reasonably accurate portrayal of "the cynodont" postcranial skeleton despite the lack of a complete and well-preserved skeleton for any given genus.

Cynodont species distinctions are so inadequately established in terms of modern systematic technique that with few exceptions the genus is the practical taxonomic unit used by most workers. Lack of samples sufficient to permit statistical evaluation is principally responsible, for many species appear to have been named without extensive comparative study. Pending a major systematic revision, trivial names are deemed unreliable. Species designations are therefore largely neglected in this study and the genus is substituted as the working taxonomic unit. This approach is also justified on the basis of the great similarity among cynodont postcranial skeletons. Among all the available postcranial materials possibly representing two or more species of the same genus, no differences could be detected that might indicate species diversity.

For each element of the postcranial skeleton discussed, an introductory section on material briefly summarizes what is available for study and which previous studies are applicable. Material cited specifically by museum or collection number is material that I have examined personally; the only exception is the type of *Leavachia duvenhagei* (RC 92), for which I had a complete series of stereoscopic photographs. Each succeeding section on morphology is a summary and comparative description of representative material. Ideally, a description of the postcranial skeleton is most informative when related to other anatomical features, especially muscles. In some cases, e.g., the humerus and femur, the comparative anatomy is sufficiently well known to permit reasonably confident reference to the muscles associated with various features. In other cases, where the disposition of muscles is in doubt, the description is necessarily strictly morphological. Following the descriptive sections, discussions of selected functional problems are appended.

I have been obliged to follow zoological (rather than anatomical) usage with regard to spelling, capitalization, etc., of anatomical terms.

Abbreviations

AMMM — Alexander McGregor Memorial Museum, Kimberley, R.S.A.
AMNH — American Museum of Natural History, New York
BMNH — British Museum (Natural History), London
BPI — Bernard Price Institute for Palaeontological Research, Johannesburg, R.S.A.
DMSW — D.M.S. Watson Collection, now housed in the University Museum of Zoology, Cambridge, England
MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
NMB — National Museum, Bloemfontein, R.S.A.
RC — Rubidge Collection, privately owned by the Rubidge family, Graaff-Reinet, R.S.A.
SAM — South African Museum (Natural History), Cape Town, R.S.A.
TM — Transvaal Museum, Pretoria, R.S.A.
UCMP — University of California Museum of Paleontology, Berkeley
UMC — University Museum of Zoology, Cambridge, England
YPM — Peabody Museum of Natural History, Yale University, New Haven, Connecticut: Vertebrate Paleontology Collection
YPMOC — Peabody Museum of Natural History: Osteology Collection

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Drs. John H. Ostrom and Edmund S. Crelin of the Departments of Geology and Anatomy, respectively, Yale University, read the manuscript in its entirety and offered criticisms that substantially improved the text. Dr. G. E. Erikson of the Division of Biological and Medical Sciences, Brown University, constructively reviewed certain aspects of the text. Dr. Robert Shapiro, Chief, Department of Radiology, Hospital of St. Raphael, New Haven, provided a critique of my discussion of the atlas-axis complex. To all of the above I express my gratitude for their participation in this study. However, I alone am responsible for any errors or faulty interpretations that might appear.

This study could not have been completed without the helpful cooperation from the staff of many museums and research institutions. In particular I would like to acknowledge: Dr. F. R. Parrington, F.R.S., for the loan of numerous specimens from the Cambridge University Museum of Zoology and from the collection of Professor D. M. S. Watson (now housed in that museum) ; Dr. J. W. Kitching, of The Bernard Price Institute for Palaeontological Research, Johannesburg, for the free use of that institute's facilities and collection of cynodonts; the late Dr. A. C. Hoffman, Director of the National Museum, Bloemfontein, for permission to study and to cast important specimens in his care; Dr. T. H. Barry, Director of the South African Museum (Natural History), Cape Town, for the use of museum facilities and for permission to study the collection of cynodonts; and Dr. A. J. Charig, of the British Museum of Natural History, for access to important type material in his department.

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The illustrations in this paper are either directly or indirectly due to the artistic skills of Carl R. Wester, Jr., of the Peabody Museum of Natural History. I am most indebted to him for preparing Figures 12, 17, 22, 24, 26, 27, 29, 31, 35, 44, 47, 48, 56, 58 and 61, and for having patience in teaching me skills sufficient to execute almost all of the remaining figures myself. His substantial contribution to this work is gratefully acknowledged. Robert J. Demarest executed the frontispiece and Robert Bakker aided in rendering Figures 5, 8, 19, 20, 40 and 42.

A. H. Coleman took the stereoscopic photographs in Figure 38, and Charles R. Schaff contributed his skills in many preparational tasks. The sagittal section of the atlas-axis complex of a 20-day-old *Didelphis marsupialis* (Fig. 9) was kindly loaned by the Wistar Institute of Philadelphia. Dr. Edmund S. Crelin of the Department of Anatomy, Yale University, provided the facilities and Elmer Newton the technical assistance that made possible the sectioning of a 25-day-old *D. marsupialis*. Louise Holtzinger and Irene Walter typed the entire manuscript at various stages in its preparation. To all of the above I am most grateful.

This study was submitted as a dissertation in 1968 to the faculty of the Graduate School of Yale University in candidacy for the degree of Doctor of Philosophy. Since that time it has been possible to make certain changes and additions, and I thank Professor Edward W. Dempsey, Chairman of the Department of Anatomy, Columbia University, for providing me with the necessary facilities. This Bulletin has been published with the aid of a National Science Foundation Publication Grant, No. GN 528.

PART ONE. POSTCRANIAL AXIAL SKELETON

1. ATLAS-AXIS COMPLEX

MATERIAL. The atlas and axis of the type of *Thrinaxodon liorhinus* (BMNH R.511) are excellently preserved and nearly complete except for the first intercentrum and portions of the arch. Incomplete atlas elements are preserved with other specimens of *T. liorhinus* (BMNH R.511a, BMNH R.3731, AMMM 5265, USNM 22812). Broom (1932b: 270) gave a diagrammatic figure of an atlas of *Thrinaxodon*.

The atlas-axis complex of *Galesaurus planiceps* is known from a specimen (UMC R.2721) described by Parrington (1934). This specimen, which subsequently has been fully prepared in acid, is one of the very few cynodonts for which the paired proatlas plates are known.

The type specimen of *Cynognathus crateronotus* (BMNH R.2571) preserves only the axis with the fused atlas centrum.

Brink (1955: 23–24) figured and described a cynodont axis (DMSW R.205) and an atlas neural arch (DMSW R. 202). He implied that these were from *Diademodon* (his paper being a study of *Diademodon*) but he never actually identified the specimens as such. In fact, the specimens are not listed in the D. M. S. Watson catalogue as positively associated with diagnostic cranial material, and therefore they must be considered generically indeterminate.[1] Kühne (1955: 99) also figured and described DMSW R.202 as *Diademodon* sp. The orientations of the arch as figured are incorrect (compare his fig. 41 with my Fig. 4).

Atlas elements positively referable to *Diademodon* are associated with a skull, the lower jaw of which was originally described as *Gomphognathus* by Janensch (1952: 237). A cast of the articulated right atlas arch and proatlas was available for study. In addition, Broom (1903) gave a complete description, including excellent figures, of both *Gomphognathus* (= *Diademodon*) *kannemeyeri* and *Trirachodon kannemeyeri*. Both of these specimens possess proatlas ossicles.

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[1] The D. M. S. Watson collection catalogue records the following information: "Collected from a small bone bed at the base of the hill immediately opposite the police station at Lady Frere. Nos. R.131–R.226 collected there, all *Diademodon*, but several spp. of different sizes may be present." However, in at least several other localities, "bone beds" containing disarticulated *Diademodon* remains also contain *Cynognathus* remains. Although Watson claimed that only *Diademodon* was represented, this fact cannot be verified because 1) the skeletal elements were disarticulated and 2) *Diademodon* cannot be distinguished as yet from other large cynodonts on the basis of postcranial anatomy.

A collection of *Cynognathus* and *Diademodon* (BPI 1675) disarticulated postcranial skeletons contains isolated and incomplete atlas-axis elements, including what is apparently the first intercentrum. In this small sample, no morphological differences could be discerned by which the two genera might be distinguished. Except for size, the atlas-axis complex of these larger cynodonts is very similar to those of *Thrinaxodon* and *Galesaurus*.

Broili and Schröder (1936: 61–63) described an axis with a fused atlas centrum, which, on the basis of associated cervical vertebrae and a cranial fragment, they believed to represent *Cynognathus platyceps*. A cast of this specimen was available for study.

ATLAS

MORPHOLOGY. The cynodont atlas consists of four separate ossifications: a centrum, two halves of the neural arch, and the first intercentrum. Broom (1903) incorrectly implied that cynodonts lack an atlas centrum; he refers to the actual atlas centrum as an "odontoid process", apparently regarding this as a derivative of the axis or second vertebra. The centrum in galesaurids (Figs. 1G, 2A, 3B) is slightly shorter anteroposteriorly than those of other cervicals; in *Thrinaxodon liorhinus* (BMNH R.511) the lengths of the atlantal and axial centra are 3.7 mm and 8 mm respectively, while in *Galesaurus planiceps* (UMC R.2721) the lengths are 6.5 mm and 8 mm respectively. The overall smaller size of the atlas centrum in *Thrinaxodon* may be partly the result of post-mortem distortion but probably also reflects some measure of actual size disparity. The anterior surface bears a large convex articular facet which is divisible functionally into four areas (Fig. 2B). The first two comprise the dorsolateral wings of the facet (*f at a*) extending posteriorly on each side and almost reaching the bases of the axis pedicles. These areas face dorsolaterally as well as anteriorly and articulate with a cup-shaped facet on each half of the atlas neural arch. The third area (*f a i*) projects ventrally and faces anteriorly and slightly ventrally; it articulates with a broad, shallowly concave facet on the posterodorsal surface of the first intercentrum. In *Cynognathus* this area is more ventrally oriented than in smaller cynodonts (Broili and Schröder, 1936). Directly above lies the fourth area which is broadly convex transversely and faces for the most part anteriorly. In some but not all specimens a faint, median swelling or tubercle occurs adjacent to the dorsal rim (*d*, Figs. 2A, B, 3C, D); the possible significance of this structure is discussed below in reference to the evolution of the dens. The tubercle and surrounding area incompletely divides the atlanto-occipital joint into separate articular areas for the incipiently differentiated occipital condyles.

The dorsal surface of the atlas centrum bears a broad, oval concavity, the surface of which is perforated by two or more nutrient foramina (*nu f*, Fig. 1G). The surface is confluent with that on the dorsal surface of the axis centrum and represents the floor of the neural canal.

The posterior face of the atlas centrum appears to be fused to the axis centrum in the types of *Thrinaxodon liorhinus* (BMNH R.511) and *Cynognathus crateronotus* (BMNH R.2571). It is difficult to be certain of the condition in the latter because of the presence of indurated matrix joining all cervical vertebrae. However, in one specimen

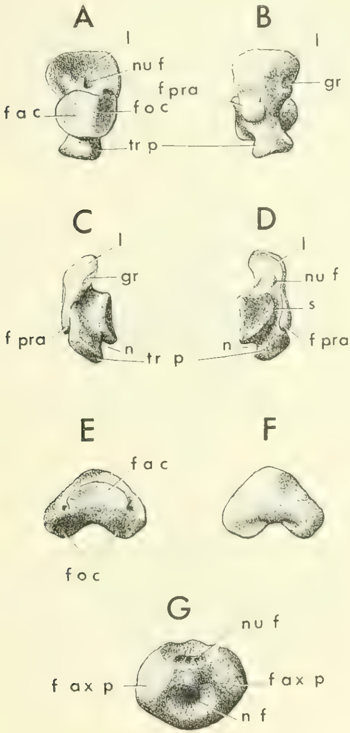

FIG. 1. Components of the atlas in *Thrinaxodon.* A, medial; B, lateral, C, posterior; D, anterior views of the left atlas arch, BMNH R. 511. E, dorsal; F, ventral views of first (or atlas) intercentrum, BMNH R. 511a. G, posterodorsal view of atlas centrum, BMNH R. 511a. Views A–D are arranged to display the total morphology and are not exactly in the anatomical "anterior", "posterior", etc., views. For the anatomically correct position of atlas arch and first intercentrum, see FIGS. 3 and 4. X2. Abbreviations for FIGS. 1–4, 6, 7, 9–11: *a a,* atlas arch; *ap,* anapophysis; *cap,* capitulum; c_1, atlas centrum; c_2, axis centrum; C_1, C_2, etc., first cervical, second cervical etc., *d,* dens; *f a c,* facet for atlas centrum; *f a i,* facet for atlas intercentrum; *f at a,* facet for atlas arch; *f at r,* facet for atlantal rib; *f ax p,* facet for axis pedicle; *f ex,* facet for exoccipital; *f o c,* facet for occipital condyle; *f pra,* facet for proatlas; *gr,* groove, possibly for muscle or ligament attachment; IC_1, atlas intercentrum; IC_2, axis intercentrum; IC_3, intercentrum of C_3; *if,* intervertebral foramen; *l,* lamina; *l r,* ridge on the lamina, possible for muscle or ligament attachment; *n,* notch for first cervical nerve and associated vessels; *n f,* notochordal fossa; *n s,* neural spine; *na,* neural arch; *nu f,* nutrient foramen; *pa,* parapophysis; *pos z,* postzygapophysis; *pra,* proatlas; *pra p,* proatlas process; *pre z,* prezygapophysis; *s,* sulcus for first cervical nerve and vessels; *s a a,* spine of the atlas arch; *tr p,* transverse process; *tub,* tuberculum.

of *Cynognathus* or *Diademodon* (BPI 1675) and in *Gomphognathus* (= *Diademodon*) *kannemeyeri* (Broom, 1903), the atlas centrum is clearly fused to that of the axis. In *Galesaurus planiceps* (UMC R.2721) the fusion is partial, with incomplete closure of the intervening suture. In other specimens of *T. liorhinus* (BMNH R.511a, BMNH R.3731), the atlas centrum has been freed of the axis through acid preparation. In posterior view these centra show a notochordal fossa identical to those developed in the amphicoelous centra of all other vertebrae (*n f*, Fig. 1G). The ventral half of the rim is a broad, rounded lip, as in other centra, which indicates that the

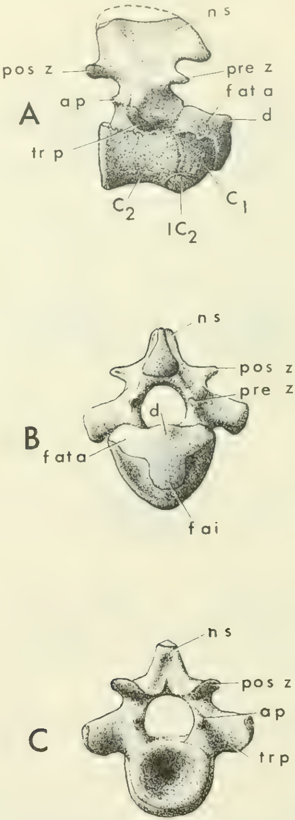

FIG. 2. The axis of *Thrinaxodon liorhinus*, BMNH R. 511. A, lateral; B, anterior, C, posterior. In this specimen the atlas centrum and the second (or axial) intercentrum are attached to the axis. X2. For abbreviations see FIG. 1.

atlas-axis articulation was not ossified and essentially the same as between other vertebrae. However, the dorsal half of the centrum lacks the broad lip which, in other centra, is continuous around the articular rim. In its place are two recessed facets (*f ax p*, Fig. 1G) on the dorsolateral corners, separated medially by a thin, horizontal plate of bone which floors the neural canal. These facets face posterodorsally and very slightly laterally and articulate with facets at the base of the axis pedicles. In *Cynognathus* and *Diademodon* this accessory articulation is obviously not developed because the atlas and axis centra are fused. In galesaurids fusion of axial with atlantal centra was probably a variable feature and perhaps dependent upon the age of the individual.

The atlas neural arch consists of two halves, the laminae of which do not co-ossify to complete the neural arch (*l*, Figs. 1, 4), contrary to the opinion of Broom (1903: 178, 1932b: 263), and of Colbert (1948: 377). There is no neural spine. Medially, each half arch bears facets for articulation with the atlas centrum (*f a c*) and one of the two occipital condyles (*f o c*), and laterally facets for articulation with the proatlas (*f pra*, Fig. 1B, D) and atlantal rib (*f at r*, Fig. 4C). A short but robust "neck" separates the two medial articular facets from the rest of the bone, imparting a greater thickness to this pedicle-lamina area than in post-atlas vertebrae. The medial facets for occipital condyle and atlas centrum are concave and more or less semicircular in outline (Fig. 1A). Their surfaces, intersecting at an angle of about 120°, are divided medianly by a low, slightly concave ridge. In *Galesaurus*, the facet for the occipital condyle is antero-posteriorly longer than the facet for the atlas centrum.

The lateral part of the atlas arch is basically a flat, straplike plate of bone which dorsally forms the lamina of the neural arch (*l*) but ventrally becomes the transverse process (*tr p*, Figs. 1A-D, 4). Above the neural canal, the lamina is nearly horizontal. The medial edge of the lamina is thin and bladelike and usually incomplete. Even in complete specimens (Fig. 3C), however, the edge does not extend medially beyond the occipital and atlas centrum facets. Therefore, the dorsomedial edges of the two halves of the atlas arch could not have met (as is true also for pelycosaurs—cf. Romer and Price, 1940: 108), and the dorsum of the neural canal was probably completed by cartilage or ligament linking the edges. The part of the lamina which projects above the occipital and atlas centrum facets is slightly concave medially and appreciably thickens ventrally. One or sometimes two foramina (*nu f*, Fig. 1A, D) occur at the junction of the plate and the "neck" supporting the articular facets for the condyle and atlas centrum. In *Thrinaxodon* (where there is consistently only a single foramen) there is no obvious exit for this foramen which evidently represents a nutrient supply.

On the dorsolateral surface of the atlas arch lamina is a broad, shallow groove (*gr*, Figs. 1B, C, 3C) which is broadest posteriorly. The lateral edge of the groove, especially in larger cynodonts, is defined by a small tuberosity. The functional significance of these two structures is not clear, especially so because there appear to be no analogous features in pelycosaurs. Possibly they represent a muscle attachment, either an atlanto-axial interarticular or one of the oblique muscles associated with the occipital joint.

In *Thrinaxodon* a rounded sulcus runs between the anterior edge of the lamina and the anterior rim of the occipital facet (*s*, Fig. 1D). The sulcus is covered by the

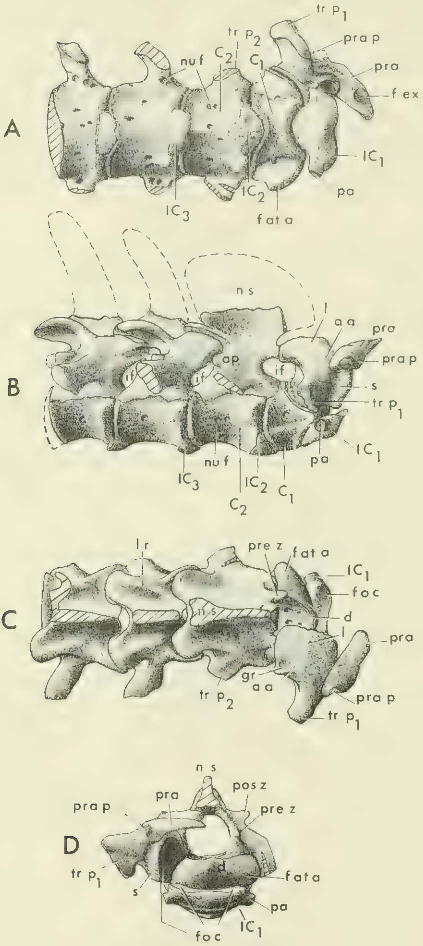
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FIG. 3. The first four cervical vertebrae of *Galesaurus planiceps*, UMC 2721. A, ventral; B, lateral; C, dorsal views. D, anterior view of atlas and axis. In this illustration the left atlas arch and proatlas have been removed to reveal details otherwise obscured. X1.6. For abbreviations see FIG. 1. Oblique hatching indicates damaged or missing bone.

proatlas, forming a short canal. Ventrally the sulcus is not covered by the proatlas; it passes posteriorly through a notch (*n*) between the transverse process and the lateral aspect of the facets for the occipital condyle and atlas centrum. The sulcus is lost as a distinct feature on the posteroventral aspect of the transverse process. In *Galesaurus* (UMC R.2721, Fig. 3B), *Cynognathus* and *Diademodon* (BPI 1675, Fig. 4A) the morphology of the sulcus is the same except that the anterior rim of the lamina contacts, and in some cases apparently synostoses with, the anterior margin of the facet for the occipital condyle. The canal is thus formed to the exclusion of the proatlas which nevertheless lies in its normal position across the area of the enclosed canal. The canal and sulcus trace the path of the vertebral artery, vein, and first cervical nerve which, in mammals, generally pass through an atlantal intervertebral foramen and alar notch. The foramen or notch in the mammalian atlas through which the first cervical nerve exits is not, of course, strictly "intervertebral"; however, it is analogous to the true intervertebral foramina and, for lack of a better term, is best designated by that name. In cynodonts, that part of the sulcus covered by the proatlas represents the intervertebral foramen of mammals, while the notch between transverse process and the rim of the medial condyles is equivalent to the alar notch of mammals. Living mammals which normally possess an enclosed first intervertebral foramen sometimes display atavistic tendencies with regard to its enclosure, thereby reverting to a primitive condition. In a specimen of *Didelphis marsupialis* (YPMOC 243), for example, the left foramen is complete but the right is open anteriorly through a failure of ossification, thus creating a deep groove similar to that in *Thrinaxodon*.

A raised, rounded facet for the proatlas is situated between the root of the transverse process and the base of lamina (*f pra*, Fig. 1B-D). The facet is slightly convex. In *Thrinaxodon* it overhangs anteriorly the sulcus for the vertebral artery and vein and first cervical nerve. In other cynodonts it often completely covers the sulcus by contacting the anterior rim of the atlantal occipital facet.

The atlantal transverse process projects posterolaterally and somewhat ventrally and its flat anterior and posterior surfaces are oriented almost vertically (*tr p*, Figs. 3C, D, 4). In most specimens the process is deeper dorsoventrally at its distal (free) end than at its base. The narrowing of the transverse process is due to the presence, across the ventral margin of its proximal end, of a notch for passage of the first cervical nerve and associated vessels (*n*, Figs. 1C, D, 4A, C). The process is otherwise rectangular, with a long, narrow facet for the atlantal rib at its distal end. The facet, which is either slightly convex or flat, faces posterolaterally and slightly ventrally. In *Cynognathus* and *Diademodon* the notch at the root of the transverse process is relatively small and does not significantly alter the outline of the process; in other respects the transverse process is like that of *Thrinaxodon* or *Galesaurus*.

In no cynodont is a transverse foramen known. In mammals, the transverse foramen pierces the posteromedial aspect of the expanded atlas transverse process for passage of the vertebral vein and artery. In some mammals, e.g., the Egyptian mongoose (*Herpestes ichneumon*), the transverse foramen pierces the dorsal surface of the atlas wing anteriorly in a fossa shared with the exit of the intervertebral foramen. The transverse foramen then traverses the length of the wing as a canal and exits at the posterior edge of the wing adjacent to the atlanto-axial joint. This and other variations of its course do not alter the basic fact that it represents enclosure of vessels by reorientation of the bone in response to new muscular requirements. The foramen obviously arose during mammalian evolution in conjunction with the expansion of the transverse process into a broad, flat wing for increased muscular attachment. Commonly the wing of the atlas extends posteriorly almost to the atlanto-axial intervertebral foramen and, during its evolutionary development, has evidently encircled the blood vessels. The shallow notch across the ventromedial aspect of the cynodont atlantal transverse process possibly represents the initial stage of formation of a transverse foramen and could have been bridged by fibrous tissue or even cartilage. In primitive mammals which do not possess a transverse foramen, e.g., *Ornithorhynchus*, *Didelphis*, there is a deep notch in the posterior border of the atlas wing which represents the incomplete development of the foramen.

The atlas intercentrum is known from *Thrinaxodon* (BMNH R.511a, Fig. 1E, F), from *Galesaurus* (UMC R.2721, IC_1, Fig. 3) and from *Cynognathus* and *Diademodon* (BPI 1675, IC_1, Fig. 4). The intercentrum is a moderately thick, wedge-shaped bone. Viewed from above or below, its outline is variable; in *Cynognathus* and *Diademodon* it is oval and somewhat irregular, in *Thrinaxodon* it is triangular, and in *Galesaurus* it is narrowly rectangular except for a protruding lip which articulates with the atlas centrum. The ventral surfaces of all intercentra are broadly convex. On its dorsal surface the first intercentrum bears a facet for the atlas centrum posteriorly (*f a c*) and two facets for the occipital condyles anteriorly (*f o c*, Figs. 1E, 4). The atlas centrum facet is oval in outline and is shallowly concave, especially along its transversely oriented long axis. This facet is confluent with part of the posterior border of the occipital facets which face anterodorsally and slightly medially. In *Thrinaxodon*, *Cynognathus* and *Diademodon*, a rounded notch in the middle of the anterior margin of the intercentrum partially separates the two occipital facets; this notch is not as deeply incised in *Galesaurus*. Each of the posterolateral corners of the intercentrum bears a posterolaterally directed parapophysis (*pa*, Fig. 4). On the apex of the parapophysis is a round or oval facet for the capitulum of the atlantal rib. A broad, flat lip, sometimes in the form of a distinct tubercle, projects posteriorly from beneath the atlas centrum facet and probably functioned in ligamentous attachment to the atlas centrum. On well-preserved first intercentra, a (?nutrient) foramen pierces the dorsal surface on either side of the facet for the atlas centrum (*nu f*, Fig. 4B). There are also foramina, variable in number, on the ventral surface, but it is unlikely that any of these communicate with those on the dorsal surface.

PROATLAS

MORPHOLOGY. All cynodonts for which the atlas arch is known have a proatlas facet, but an intact proatlas ossicle is a rarity. A proatlas ossicle is preserved in articulation with the atlas arch and occiput in a Munich Museum specimen of *Gomphog-*

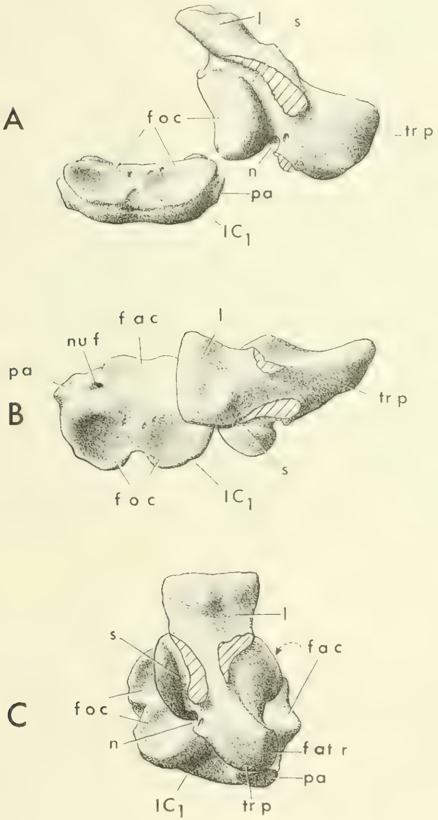

FIG. 4. The first intercentrum and left atlas arch of cf. *Cynognathus* (*?Diademodon*), BPI 1675. A, anterior; B, dorsal; C, lateral views. The two elements are probably not from the same individual. They are arranged in the approximately correct anatomical relationship. X1. For abbreviations see FIG. 1. Oblique hatching indicates damaged or missing bone.

nathus (= *Diademodon*), the lower jaw of which was described by Janensch (1952: 237). Proatlas ossicles are described by Broom (1903) in *Gomphognathus* (= *Diademodon*) *kannemeyeri* and in *Trirachodon kannemeyeri.* A proatlas is known in one specimen of *Thrinaxodon* (USNM 22812). Proatlas ossicles are also preserved in a specimen of *Procynosuchus* in the Rubidge Collection (A. W. Crompton, personal communication) but I have not examined this specimen. Parrington (1934) described and figured the proatlas ossicles of *Galesaurus planiceps* (UMC R.2721). Parrington's description requires modification in light of the additional preparation undertaken on this well-preserved specimen.

In outline the proatlas ossicles of *Galesaurus* are trapezoidal (*pra*, Fig. 3B, C), not rhomboidal as originally described and figured. The slightly concave ventral margin is more or less horizontal and is the thickest part of the plate. On the lateral surface, halfway along the ventral margin, is a process that has been broken off on both sides (*pra p*, Fig. 3A-D). Parrington incorrectly figures this tuberosity at the junction of the ventral and anterior margins of the plate. The process is well preserved in the specimen of *Diademodon* described by Janensch (1952) and is well known in the South American traversodontid *Exaeretodon* (Bonaparte, 1963a). In the former the process is rectangular in cross-section, dorsoventrally compressed and wider anteroposteriorly. In length it slightly exceeds that of the atlas transverse process and therefore extends laterally beyond the tip of the atlas transverse process.

The anterior and posterior margins of the proatlas ossicle of *Galesaurus* are approximately parallel and incline cranially at an angle of about 20° from the vertical. The convex anterodorsal margin is the thinnest part of the plate. The plate as a whole is bowed and slightly twisted so that the ventral (or lateral) half faces dorsolaterally while the dorsal (or medial) half faces posterodorsally. The internal surface of the plate bears two facets, one at its posteroventral corner for articulation with the atlas, the other near the junction of its anterior and anterodorsal margins for articulation with the exoccipital (*f ex*, Fig. 3A).

Axis

MORPHOLOGY. The second or axial intercentrum has been recovered only with articulated specimens and thus the morphology of its articular surfaces is not completely known. It is best preserved in *Galesaurus planiceps* (UMC R.2721, *IC*$_2$, Fig. 3A, B). Like other intercentra, it probably has the general structure of a curved plate. The ventral surface, diamond-shaped in outline (Fig. 3A), is convex transversely as well as anteroposteriorly. The anterior edge is markedly convex and the posterior rim of the atlas centrum is reflected anteriorly to receive it. The posterior edge is nearly straight except for a slight backwardly projecting tubercle.

The axis centrum of cynodonts is similar to the centra of other postaxial cervical vertebrae (*C*$_2$, Figs. 2, 3). Presumably the centrum was amphicoelous, although fusion or attachment by matrix to the atlas centrum prohibits examination of the anterior face of any known axis centrum. The lateral sides of the centrum are concave anteroposteriorly, meeting along the midventral line to form a keel. The sides are perforated by a number of nutrient foramina (*nu f*) in variable patterns. The dorsum of the centrum is beveled by three surfaces, two of which are dorsolateral and join with the pedicles, the third lying between the two and forming a broad groove for the floor of the neural canal. In the center of the canal floor is a fossa of unknown function which is similarly developed in all other postaxial centra. Broili and Schröder

(1936: 64–65) observed the same feature in cynognathid cervical vertebrae. They discussed the possibilities that it was related to the "marrow cavity" (actually, cancellous bone) of the centrum or that it formed as a result of an unusual pattern of synostosis of the neural arch to the centrum. At present, neither of these possibilities can be given a definitive evaluation.

The pedicles of the axial arch join the centrum along its entire length except posteriorly where the rim of the centrum is continuous about the entire articular face. The anterior quarter of each pedicle overhangs the anterior articular face of the axial centrum and articulates, at an angle of about 45° from the horizontal, with the posterolateral corners of the atlas centrum. The articulations between the pedicles and both centra appear to be synchondroses. The articulation between atlas and axis centra, and the contact between axial pedicles and atlas centrum, are apparently partially synostosed in one specimen of *Thrinaxodon liorhinus* (BMNH R.511).

The transverse processes of the axis are robust and rectangular. They project laterally and somewhat posteroventrally, each bearing on its slightly swollen terminus an oval facet for the tuberculum. The orientation of the transverse processes are more horizontal than are those of post–C2 vertebrae (Fig. 3B).

The prezygapophyses, diminutive in size compared to the postzygapophyses, are not preserved in most specimens. In *Thrinaxodon liorhinus* (BMNH R.511) and *Galesaurus planiceps* (UMC R.2721), the processes are thin blades which attenuate to a blunt point (*pre z*, Figs. 2A, 3C). Their orientation conforms to that of the laminae from which they arise, i.e., the external surface facing dorsolaterally, the internal facing ventromedially. In neither *T. liorhinus* nor *G. planiceps* can distinct articular facets be detected on these processes. The postzygapophyses are robust and bear facets which incline ventrolaterally at an angle of about 45° (*pos z*, Fig. 2). Beneath each postzygapophysis is an anapophysis (*ap*, Figs. 2A, C, 3B) which projects posteriorly from the pedicles at the level of the top of the transverse process. In recent mammals, anapophyses usually represent the point of insertion of a part of the longissimus muscle system.

The spinous process or neural spine is a broad, hatchet-shaped blade (*n s*, Figs. 2, 3). In cross-section it is very thin through the middle, but both anteriorly and posteriorly it is much increased in thickness and is terminated, at the anterior end at least, by a tuberosity. In *Thrinaxodon* and *Galesaurus*—the only two genera for which nearly complete spines are known—there are two fossae for muscular origin on each side of the blade. One is just above the base of the prezygapophysis; the other lies more or less in the center of the blade surface. In all known specimens the thin dorsal edge of the blade is at least partly lost. Brink (1954: 117) described the dorsal edge in *Thrinaxodon liorhinus* (NMB C.392)[2] as concave. However the specimen to which he referred is broken in this area. The type of *Thrinaxodon liorhinus* (BMNH R.511) is less damaged and shows that the edge was at least straight and probably convex.

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[2] Erroneously listed by Brink (1954) as C.292, although his caption to text-figure 1 correctly labels it C.392.

Atlantal and Axial Ribs

MORPHOLOGY. It is certain that both the atlas and the axis of cynodonts bear ribs because the shape of their transverse processes is no different from those of other rib-bearing cervical vertebrae. Parrington (1934: 48) described a rib associated with *Galesaurus planiceps* (UMC R.2721) which he believed to be an atlantal rib. Further preparation (in acid) on this specimen has been undertaken since Parrington's original description, and, as this remains the only known rib associated with the first two cervical vertebrae, further description is warranted.

Originally the complete rib was 9 mm long and 4 mm wide at its midpoint, expanding distally to a spatulate terminus. The proximal end was lodged between the atlas transverse process and the atlas centrum and was thus obscured. With further preparation the distal end was lost but the proximal end was freed. The proximal end is a very thin, spatulate plate averaging 0.8 mm in thickness. There is no rodlike thickening anywhere on the plate to denote a central axis or shaft. The tuberculum is a rectangular process which projects only a short distance from the plate. The tubercular facet is 3 mm long, not 3.5 as reported by Parrington, is approximately 1 mm wide at its dorsal end, and is constricted in the middle which imparts a figure 8 outline. The facet of the atlas transverse process has a similar outline, but is almost 5 mm long and, at the dorsal end, 2 mm wide. This disparity in size is difficult to account for unless there was a considerable amount of cartilage or connective tissue intervening. The capitulum is a small tubercle located on the ventral margin of the plate, 2 mm from the base of the tuberculum. Its diameter is about half that of the parapophysis on the atlantal intercentrum. This disparity in size is similar to the anomalous tuberculum-diapophysis relationship and must have required an unusual amount of connective tissue or cartilage to complete the articulation. The rib has been somewhat crushed, but it appears probable that its platelike surface was slightly concave medially and convex laterally.

2. THE EVOLUTION OF THE MAMMALIAN ATLAS-AXIS COMPLEX

Specializations of the cynodont atlas and axis represent an initial stage in the evolution of a mammalian atlas and axis. In order to evaluate these specializations, reference must be made to the atlas-axis structure and function in pelycosaurs as well as in mammals. For clarity, separate consideration is given to each of the major functional aspects of the atlas-axis joint.

The Position of the Occipital Condyles

The most obvious difference between reptiles and mammals at the atlanto-occipital joint lies in the condyles—reptiles being monocondylic and mammals bicondylic. Equally obvious is the fact that the mammalian condition is derived from the reptilian by a "splitting" of the originally single condyle. The position of the mammalian condyles is not so easily explained, for they invariably occur lateral to the foramen magnum. If the course of condylar evolution had been a process of simple bisection, the expected position of the two mammalian condyles would be ventrolateral to the foramen magnum. But mammalian condyles have apparently migrated dorsally as well as laterally. In cynodonts, the position of the condyles with respect to the foramen magnum is not quite mammalian and in fact is intermediate between an early synapsid (pelycosaur) stage and that of a typical mammal. The shift in the position of the condyles with respect to the foramen magnum is almost certainly related to other mammalian specializations of the atlanto-occipital joint. The most important of these specializations involves an increased ability to flex and extend the head.[3] Therefore, the position of mammalian condyles is also possibly related to an increase in the range of flexion and extension—as the following functional analysis attempts to demonstrate.

The single occipital condyle of pelycosaurs is convex, with a subcircular, often nearly triangular, outline (Fig. $5A_2$). It is composed of equal contributions from the paired exoccipitals and a median basioccipital and lies directly beneath the foramen magnum. When the head flexes or extends, the axis of cranial movement is a theoretical line drawn transversely through the condyle. The spinal medulla, lying entirely above the axis of movement, must be compressed during extension and stretched during flexion. For x degrees of flexion, for example, the amount of spinal medulla elongation is given by

$$2\pi r\left(\frac{x}{360}\right)$$

where r is the distance between the axis of rotation and a selected point in the spinal cord. This assumes that stretching occurs along an arc. If the elongation is linear, then the amount is given by

$$\cos\frac{x}{2}=\frac{\frac{x}{2}}{r}$$

and is slightly less. Spinal cord deformation at the reptilian atlanto-occipital joint is the result of a large r value, which is constant for any selected point, and a variable x (degrees of flexion) value.

There is no comparative data on the elastic limits of tetrapod spinal medullae. However, in terms of specializing for maximum extension and flexion, an obvious mechanical advantage results from a reduction of the value of r so that the amount of spinal medulla deformation per degree of flexion or extension (x) is minimized. Such a reduction is possible if the spinal medulla intersects the axis of flexion and extension by "passing through" the occipital condyle. In this case the r values vary from zero (at the intersection of the rotational axis and the spinal medulla) to an amount equal to the radius of the spinal cord itself. Thus, for a given diameter of spinal medulla, values of x produce the least deformation possible. Mammals have evolved precisely this

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[3] Flexion and extension are here employed with respect to the head and neck as in human anatomy. Flexion is movement downward and forward, extension is movement upward and backward.

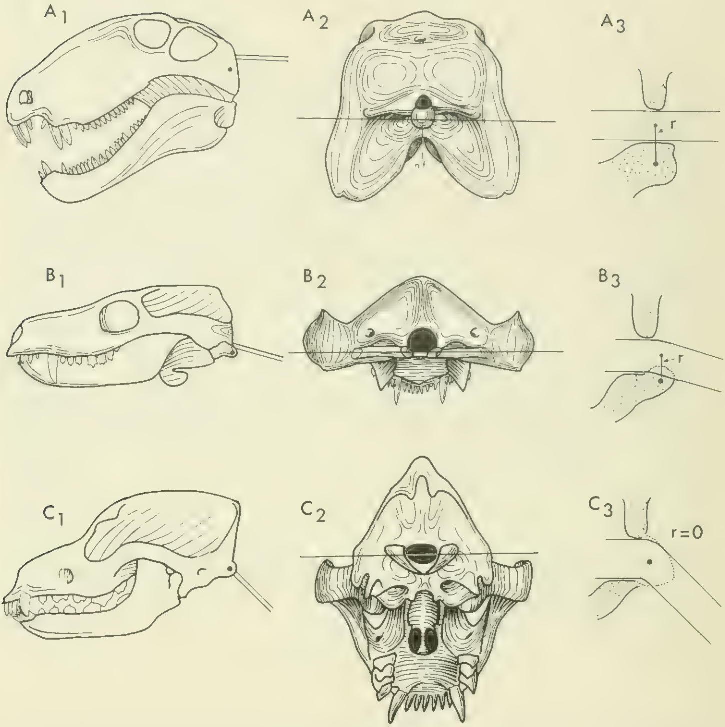

FIG. 5. Diagrammatic representation of A, *Dimetrodon*; B, *Thrinaxodon*; and C, *Canis*, representing stages in the evolution of mammalian occipital condyles. Subscript 1, lateral view of skulls with double line indicating position of spinal medulla relative to transverse axis of flexion-extension, represented by black dot. Subscript 2, occipital view of skulls, i.e., looking along spinal medulla into foramen magnum, with single line representing the transverse axis of flexion-extension. Subscript 3, sagittal sections through the foramen magnum. r = vertical distance between axis of flexion-extension and the center of the spinal medulla. Not to scale.

arrangement (Fig. $5C_3$). The position of the condyles lateral to the foramen magnum entails the passage of the axis of flexion and extension through or close to the spinal medulla center. This relationship, one of the most invariable of mammalian anatomy, accounts for the lateral position of the condyles relative to the foramen magnum.

The occipital condyles of most cynodonts are clearly separate[4], but they do not occupy a typically mammalian position. Instead, cynodont condyles occur at the ventrolateral "corners" of the foramen magnum (Fig. $5B_2$; see Brink and Kitching, 1953b, for *Cistecynodon*; Broili and Schröder, 1934, for *Cynognathus*; Brink, 1954, for *Glochinodontoides*). In this position, the axis of flexion and extension is nevertheless relatively closer to the spinal medulla than it is in pelycosaurs and is intermediate between the basic reptilian and mammalian patterns.

These conclusions are similar to those reached by Hayek (1927: 334–336), but were independently derived. Hayek noted that in living amniotes the axis of flexion and extension—his "frontal Bewegungsachse"—is variable in position with respect to the foramen magnum. He was able to show, using both osteological models and cadavers, that in birds (essentially as in Fig. 5A) there is considerable displacement of a point marked on the spinal medulla during flexion and extension. Employing the same technique in the study of cervico-occipital flexion and extension in man (as in Fig. 5C), he found essentially no displacement. While Hayek's data are consistent with the analysis given here, neither demonstrate the basis for the necessity of limiting spinal medulla or medulla oblongata deformation in mammals. Either the elastic properties of the spinal medulla are approximately the same in the two classes, in which case other factors require the elimination of deformation at this joint in mammals, or the elastic properties are not the same, in which case the mammalian arrangement of condyles is an adaptation for maximum movement and minimum deformation. At present there are no data on which to base a choice between these alternatives.

Cervico-Cranial Flexure and the Position of the Atlanto-Occipital Joint

The evolution of a bicondylic occipital joint in mammals is accompanied by certain postural changes of the head and neck. In most mammals, the axis of the cervical vertebral series ascends toward the skull (Fig. $5C_1$). The longitudinal axis of the skull, however, is normally inclined in an opposite direction, so that the rostral end of the skull is lower than the occipital end (see de Beer, 1947). Hence there is an angulation between the cranial and cervical axes. This feature is also accompanied by a relative displacement of the foramen magnum and occipital condyles to the extreme posteroventral aspect of the skull (Fig. $5C_2$). In most Paleozoic as well as in many recent reptiles, the cervical axis is nearly horizontal and more or less continuous with the longitudinal cranial axis; in normal posture the head is little or not at all elevated above the level of the axial skeleton (Fig. $5A_1$). The atlanto-occipital articulation is located at or near the midpoint of the occipital surface so that there is about as much cranial mass above the occipital condyle as below it (Fig. $5A_2$). These basic relationships, which in reptiles actually are not much advanced beyond a piscine stage, not only limit flexion and extension, but provide a relatively short moment arm for extensor musculature with which head posture is maintained. The anatomy of the mammalian

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[4] Procynosuchids have a kidney-shaped condyle which is only incipiently bicondylic; see Brink (1963: 60).

atlanto-occipital articulation is partly explicable in terms of permitting greater freedom in extension and flexion and providing a longer lever arm for extensor musculature.

In generalized mammals where the normal curvature of the spine in the anterior thoracic and posterior cervical regions results in an ascending axis toward the skull and the longitudinal axis of the skull is characteristically oriented in the opposite manner, the spinal medulla does not exit from the foramen magnum in a strictly caudal direction. Instead, it passes posteroventrally to conform with the descending neural canal. The condyles and foramen magnum are located more or less at the juncture of the occipital and basioccipital surfaces. This arrangement, associated with the angulation of the cranial and cervical axes, provides a relatively greater amount of space for flexion and extension than does the reptilian arrangement (compare Fig. $5A_1$ and $5C_1$). Cynodonts appear to be more mammalian than reptilian with regard to the location of the occipital condyles, and in *Thrinaxodon* at least, the foramen magnum is directed posteroventrally, which indicates angulation of the cranial and cervical axes (Fig. $5B_1$). It is difficult to be positive about the posture of the neck in cynodonts. The relatively high neural spines of the cervical series are consistent with an interpretation of well-developed extensor musculature, but do not necessarily establish an ascending cervical axis. From evidence of the angulation of cranial and cervical axes, it appears likely that the cynodont head and neck were at least somewhat elevated, thus approximating a mammalian condition. The parasagittally oriented zygapophyses of the anterior thoracic vertebrae would certainly permit such a posture.

The Origin and Homology of the Dens

Cynodonts do not possess a typical dens, or odontoid process, which in mammals forms a toothlike or tonguelike projection of the axis into the atlas ring. Nevertheless, the cynodont atlas-axis complex is important to an understanding of the structural evolution of the dens and, together with certain osteological and developmental evidence from mammals, clarifies its homology. Standard reference works of mammalian anatomy state that the dens is shown developmentally to represent the atlas centrum (e.g., Sisson and Grossman, 1953: 32; Young, 1957: 150; Crouch, 1965: 145; etc.). In fact, the development of the dens is more complex than has been generally acknowledged and it is necessary to review the embryological evidence in some detail before considering its evolutionary history.

Goodrich (1930: 69–70) summarized the evidence supporting the conclusion that in certain reptiles, birds and mammals, the dens (or, in reptiles, the atlas centrum) forms from two chondrification centers. Goodrich concluded, following other authors, that the anterior chondrification center represents an anterior sclerotomite; the posterior sclerotomite of the same sclerotome enters into the formation of the atlas. Thus the proatlas is the neural arch (dorsal half) ossification of this anterior sclerotomite, and the anterior chondrification center of the dens is the pleurocentral (ventral half) manifestation of the same anterior sclerotomite. The contribution of a "pro-atlantal" sclerotomite to the tip of the dens has subsequently been confirmed in *Mus* (Dawes, 1930), in *Peromyscus* (Sensenig, 1943) and in man (Sensenig, 1957). Hayek's (1924) observation that in reptiles the ventral half of a "pro-atlantal" sclerotomite contributes to the anterior half of the atlas centrum establishes that this developmental process is basically the same as in mammals. Therefore, there was no radical modification in development during the reptilian-mammalian transition. The remainder of the dens, i.e., its posterior chondrification center, is universally acknowledged to be derived from sclerotomic material homologous in position to the sclerotomic material which gives rise, in reptiles, to the atlas centrum. On this basis the developmental equivalence of the mammalian dens with the reptilian atlas centrum is established.

The supposedly well-established developmental history of the dens still does not account for the evolution of its characteristic shape and relations. For example, if the dens is a structurally altered atlas centrum, then what selective processes account for its diminution and encapsulation into the atlanto-axial joint? Furthermore, the developmental evidence has never been used to define the exact contact between the axis centrum and dens ("atlas centrum"). Apparently neither of these aspects is well understood. Romer (1962: 172) stated that the dens also includes the intercentrum of the axis, while Lessertisseur and Saban (1967: 601) admitted the additional possibility that the axial intercentrum may be completely lost. Miller et al. (1964: 52) claimed that in the dog the dens "is morphologically the caudal part of the body of the atlas. . .", implying thereby that a cranial part has not been accounted for or is lost. Authors seldom define a line of separation between dens ("atlas centrum") and axis centrum. Since, however, the dens is invariably equated with the whole of the atlas centrum (plus a proatlas rudiment), the obvious conclusion would be that the division of dens from axis centrum occurs at the base of the dens.

The homology and structural evolution of the dens is clarified by reviewing the basic features of the pelycosaur, cynodont and monotreme atlas-axis complexes. In pelycosaurs and cynodonts, the atlas centrum is clearly a separate ossification and alone bears the facets which articulate with the two halves of the atlas arch. The atlas centrum of these forms is primitive insofar as its dimensions approximate those of other cervical centra, the only exception being that in length it is somewhat shorter than other centra.

In pelycosaurs a notochordal remnant was present in the atlanto-occipital joint, for both the occipital condyle and anterior face of the atlas centrum bear a slight notochordal fossa just above center (Romer and Price, 1940: 64; *n f*, Figs. $5A_2$, 6C, D). This notochordal remnant might have been in the form of a nucleus pulposus, such as typically occurs in mammals between all vertebrae except in the sacral, atlanto-occipital and atlanto-axial joints. If this were the case, a true synovial joint was not present, but rather an amphiarthrodial joint in which a fibrocartilaginous disc (perforated through the center for the nucleus pulposus) connected occiput to atlas centrum. This type of joint would have greatly restricted the range of movement. However, it appears more likely that at least some form of synovial capsule in this region was part of the heritage of early synapsid reptiles. Romer and Price (1940: 108) concluded that in pelycosaurs most movements of the head with the atlas-axis joint occurred at the altanto-occipital joint. In order for this simple ball-and-socket joint to have permitted even limited degrees of flexion, extension, abduction and rotation, a synovial joint of some sort must have been present. Furthermore, a synovial joint would be required by the apparently close apposition of the anterior surface of the atlas centrum, arches and intercentrum with the occipital condyle (except, of course, the small notochordal pit on each side). In typical post-C2 vertebrae, however, the centra are deeply amphicoelous and notochordal. The adjacent rims of these centra lack the finished surface typical of bone covered with articular cartilage and were probably bound together by ligaments (Romer and Price, 1940: 96) as in the annular ligaments of mammals. Smoothly textured bone is evidence of articular cartilage and hence a synovial cavity. The occipital condyle and anterior surface of the atlas centrum possess just such surfaces, and therefore it is reasonable to conclude that some sort of a synovial capsule, with its typical membranes and fluid, was already developed in pelycosaurs. If the atlanto-occipital joint in pelycosaurs were of a synovial type, then the notochordal pits still remain to be explained. Possibly they functioned in attachment of an atlanto-occipital ligament within the synovial capsule. Ligaments within an articular capsule, e.g., the cruciate ligaments of the knee, are known to be an important mechanism for maintaining joint integrity and control.

Whether the notochordal pits of pelycosaurs represent a gelatinous or ligamentous remnant, there is no question that the pits are absent in cynodonts and that their associated structure must have been altered or displaced. With the doubling of condyles, the notochordal pit of the originally single condyle is of course lost. The area on the anterior face of the cynodont atlas centrum corresponding to the position of the pelycosaurian notochordal pit is smooth, with no sign of an indentation (Fig. 2B). The only possible structural manifestation of a notochordal rudiment is in a slightly more dorsal position, at a level just below the floor of the neural canal. In *Thrinaxodon* (BMNH R.511, BMNH R.511a) and *Galesaurus* (UMC R.2721), a slight protuberance occurs at the point, here interpreted as an incipient dens (*d*, Figs. 2A, B; 3C, D). As a median structure separating the two lateral facets for the neural arch halves, it lies in a position analogous to that of the mammalian dens. A similar feature is present on two other axes (DMSW R.204, DMSW R.205) of large, unidentified cynodonts, probably, but not certainly, *Diademodon*, and also on a separate atlas centrum from either *Cynognathus* or *Diademodon* (BPI 1675). An incipient dens has also been identified in the South American traversodontid *Massetognathus pascuali* (Jenkins, 1970a). This proturberance is not found in all known cynodont axes but it is so subtle a feature that it easily might be lost through plastic deformation of the fossil or through careless preparation. After examining a cast of Broili and Schröder's (1934) ?*Gomphognathus* axis, which does not show this feature, I have concluded that this specimen has undergone deformation. The type of *Cynognathus crateronotus* (BMNH R.2571), which also lacks this feature, has been somewhat crudely prepared.

The generally held belief that the mammalian dens represents the atlas centrum has led several authors (e.g., Seeley, 1895b) to refer to the entire atlas centrum in therapsids as a dens. Lessertisseur and Sigogneau (1965) claimed that dinocephalians, dicynodonts and cynodonts all possess an "apophyse odontoide". Were these authors referring to the atlas centrum or some peg-like process of the axis? The atlantal centra of the dinocephalians and dicynodonts that I have examined are generally similar to those in pelycosaurs and do not warrant the term odontoid process; there is no trace of a dens in these forms. Hoffstetter and Gasc (1969) used the terms odontoid process and atlas centrum interchangeably in reference to the atlas centrum of living reptiles. This nomenclatural synonomy should be avoided if the odontoid process (or dens) and atlas centrum of mammals are not exactly equivalent structures (as will be demonstrated more fully below). The distinction is all the more important in view of the possibility that some reptiles have independently evolved a dens and ligaments analogous to those in mammals (see p. 41).

Developmentally the mammalian dens is intimately associated with a notochordal remnant which becomes the apical ligament (cf. Goodrich, 1930: fig. 61; Gadow, 1933: 95, 311; Gray, 1959: 355). The apical ligament connects the apex of the dens with the basioccipital. The evolutionary history of the notochordal remnant between occiput and atlas is therefore quite different from that between other vertebrae, where it forms the nucleus pulposus (see Williams, 1908). Not only are there obviously different structural specializations represented, but also the relative positions of the two are not the same. The nucleus pulposus retains its primitive position along an axis which pierces the centers of the centra. The notochordal segment that is represented by the apical ligament has apparently migrated dorsally so that it no longer occupies a precisely intercentral position. This migration was already underway in pelycosaurs, for the notochordal fossa is slightly above center on the anterior face of the atlas (*n f*, Fig. 6C, D). In cynodonts further migration carried the notochordal remnant still more dorsally to a level just below the floor of the neural canal, approximating the mammalian condition. During the pelycosaur-cynodont transition, the structure (as well as the function) of the notochordal remnant was altered. In pelycosaurs the notochordal remnant probably retained some of the characteristics of a primitive notochord, being enclosed in a reduced but nevertheless primitive amphicoelous

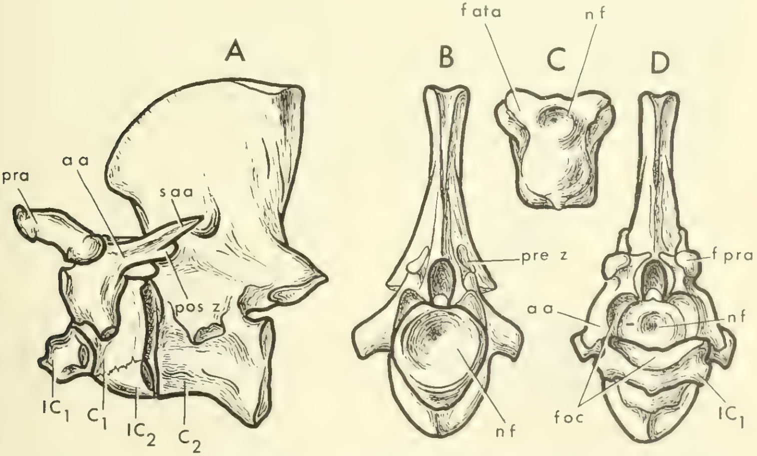

FIG. 6. The atlas and axis of the pelycosaur *Ophiacodon retroversus*, after Romer and Price, 1940: fig. 44. A, lateral view of complete atlas-axis complex. B, anterior view of axis. C, anterior view of atlas centrum. D, anterior view of atlas-axis complex, proatlas ossicles removed. X0.7. For abbreviations see FIG. 1.

concavity. In cynodonts a basic alteration of the structure of the notochordal remnant would account for the loss of the notochordal fossa and the development of an incipient dens. An "apical ligament" probably extended to the basioccipital between the condyles, thus strengthening the atlanto-occipital articulation. At a later and as yet unknown stage the caudal part of the ligament may have been strengthened by ossification in situ or, with the same result, replacement by an increasingly longer protuberance of bone from the body of the atlas centrum. Whatever were the caudal processes in the development of a dens, selection pressures for its development must have been high once the possibility of rotation at the atlanto-axial joint was realized. A tonguelike or toothlike dens is one of the most invariable features of the mammalian postcranial skeleton. Among modern mammals, only some cetaceans lack a dens.

The dens is unquestionably one of the earliest definitive structures to appear in mammalian phylogeny: Kermack (1963) reported a "fully formed odontoid" in the Late Triassic mammal *Morganucodon*. Kühne (1956) described and figured a dens of mammalian proportions in the Liassic tritylodontid *Oligokyphus*. Although *Oligokyphus* is not a mammalian ancestor, but a specialized and late-surviving therapsid, the morphology of the axis is exactly what would be expected in a mammalian ancestor: the atlas centrum is fused to the axis centrum, as in some cynodonts and in all mammals. But in place of the slight protuberance of cynodonts is a typically mammalian dens. This may be termed the "prototherian" stage in the evolution of the dens and will be now considered with reference to *Ornithorhynchus*.

The final stage in the evolution of the dens is represented by the *Ornithorhynchus* dens, which in morphology and size is entirely mammalian (*d*, Fig. 7). However, the relationship of the dens to the axis centrum is not typically mammalian because these elements are widely separated by a bulbous ossification (C_1, Fig. 7) that bears articular facets for the atlas. In a typical mammalian axis, the dens and cranial articular facets abut against the axis centrum more or less directly beneath the anterior limit of the axis neural arch; the dens and cranial articular facets are not widely separated from the axis centrum. Is the bulbous ossification between dens and axis centrum in *Ornithorhynchus* developed from materials of axis centrum or atlas centrum deriva-

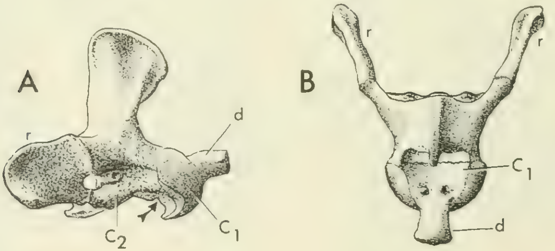

FIG. 7. Axis of a platypus, *Ornithorhynchus anatinus*, YPMOC 5123. A, lateral view; B, dorsal view. Specimen is that of a young adult. Arrow in A indicates the joint between axial and atlantal centra; the same joint can be seen in B running across the floor of the neural canal behind the anterior articular facets for the atlas. X 2. Abbreviations as in FIG. 1 except: *r*, axis rib.

tion? This leads to the crucial question of the homology between the mammalian dens and primitive atlas centrum.

The purported homology between the mammalian dens and the atlas centrum of lower tetrapods was probably first formulated by Cuvier[5]. Among the many workers to investigate the atlas-axis complex, only Ludwig (1954) challenged Cuvier's concept. From serial sections of early human embryos, Ludwig concluded that the dens arose directly from the axis body and that no homologue of the atlas body exists. However, Ludwig's figures show that he misinterpreted his material and that an atlas body is indeed present in humans (Jenkins, 1969: fig. 2F). Kladetzky (1955) gives other criticism of Ludwig's theory. The general acceptance of Cuvier's homology is due to developmental evidence unequivocally demonstrating that the dens is formed from sclerotomic cells in the position expected of the atlas centrum. Heretofore, fossil evidence neither confirmed nor denied this seemingly simple relationship. If Cuvier's homology is taken at face value, then the atlas centrum, originally the diameter of other cervical centra, became progressively smaller during the course of mammalian evolution until only a vestige remained as the peglike dens fused to the axis. In this case the atlas centrum is represented only by the dens. But this view is untenable in face of the evidence that cynodonts possessed both an incipient dens and an atlas centrum of primitive, large size (see above). More important, this view does not account for the origin of the anterior articular facets of the mammalian axis. In both pelycosaurs and cynodonts the posterior facets of the atlas arches articulate only with the atlas centrum. Therefore, there is the possibility that at least the cranial articular facets on the mammalian axis, articulating with the homologues of the atlas arches, represent part of the original atlas centrum. An unknown amount of the supposed axis "centrum" caudal to these facets may also represent the original atlas centrum. No further paleontological evidence is available which supports this hypothesis, but the joints in the axes of recent mammals provide positive confirmation of the presence of part of the primitive atlas centrum posterior to the dens.

In no mammalian axis is there a trace of any joint between the base of the dens and the cranial articular facets, as would be expected if the dens alone were the rudiment of the atlas centrum. In the axis of young mammals, a joint divides the axis transversely and is here interpreted as demarcating the axial and atlantal moieties. This joint, variable in position, apparently closes in early postpartum life. In the monotreme *Ornithorhynchus anatinus* (Fig. 7), the joint lies posterior to the cranial articular facets. With exception of its typically mammalian dens, the *Ornithorhynchus* axis is therefore constituted very much like a cynodont axis. The anterior ossification of *Ornithorhynchus* retains approximately the same anteroposterior length relative to the axis centrum as occurs in the atlas centrum of cynodonts. This anterior ossification, homologous with the body of the atlas, alone bears the cranial articular surface for the atlas as in cynodonts. This surface is composed of two dorsolateral facets, one for each half of the neural arch, and a ventromedial facet for the atlas intercentrum—an arrangement which is essentially the cynodont condition. The monotreme axis is primitive because it retains a relatively extensive articulation between the homologues of the atlas centrum and intercentrum. Typically in more advanced mammals this articulation has been reduced or lost in favor of a new contact between the dens and atlas intercentrum.[6] The primary contact of a metatherian or eutherian axis with the intercentrum ossification is via the ventral surface of the dens which extends dorsally over the intercentral part of the atlas ring. *Ornithorhynchus* and, to a lesser extent, *Tachyglossus* retain both the primitive, ventromedial facet for the atlas intercentrum and the specialized "mammalian" contact via the dens.

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[5] Discussing the origin of the concept of a dens-atlas centrum homology (Jenkins, 1969), I believed that Cuvier initially formulated the general idea about 1835 but that Bergmann, Rathke and Owen, among others, were the first to equate the two structures in the sense of homology. Further investigation has revealed that Cuvier made specific deductions concerning the equivalence of the dens and atlas centrum that antedate those of the above mentioned authors, although the term "homology" (with the implication of evolutionary continuity) was not used. In 1808 Cuvier wrote of the crocodilian axis: "A la face antérior du corps, se joint par un cartilage, une pièce convexe à cinq lobes . . . qui tient lieu d'apophyse odontoïde par son lobe moyen. . . ." Cuvier (1824) later made a definitive statement regarding the atlas centrum in turtles: "Cette pièce, analogue à celle que nous avons déjà vue dans le crocodile, représente l'apophyse odontoïde de l'axis des mammifères. . . . Ce qui prouve que cette pièce, analogue à l'odontoïde, est dans le fait le corps de l'atlas."

In *Tachyglossus aculeatus* (Fig. $8G_1$, G_2) the axis is somewhat more specialized and less cynodont-like than in *Ornithorhynchus*. A small part of the cranial articular facets is borne by the axis neural arches and the ventromedial facet for the (atlantal) intercentral ossification is reduced in size. These incipient specializations are further developed in metatherians and eutherians. Gaupp (1908) studied the development of the atlas-axis complex of *Tachyglossus* in detail. He concluded that the atlas body not only contributed to the formation of the dens, but also to the cranial half of the definitive axis body. His study confirms the present account of the monotreme atlas body forming the major part of the cranial articular facets of the axis—as was the case among cynodonts.

In representative genera of all living families of marsupials, a transverse joint divides the axis body in juveniles. The joint usually occurs entirely posterior to the cranial articular facets, although in a few cases the joint appears to transect the dorsolateral corner of the facets. The joint in marsupials is similar to that in *Ornithorhynchus* or *Tachyglossus* and may be considered as a retention of a primitive condition. However, marsupials share with eutherians the tendency to reduce or lose the ventromedial facet for the atlantal intercentrum (the ventral arch of the atlas ring), so that the ventral surface of the dens is the principle contact of the axis with the ventral atlantal arch. Despite this specialization, marsupials retain a substantial postdens component in the axis that is homologous with the primitive atlas centrum.

The axis of eutherian mammals shows a wide range of morphological variation between orders and even between families. Among juveniles, a transverse joint invariably occurs that separates the dens and a postdens component from the body of the axis. This joint usually transects the cranial articular facets, but not always so as to bisect them. In the dog (Fig. 8D) and Indian elephant (Fig. 8F), the joint divides

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[6] In most mammals the atlas intercentrum is represented by a ventromedian center of ossification in the atlas ring. It usually fuses with the two halves of the neural arch to complete the ring but may persist in the adult as a separate ossicle (e.g., *Thylacinus*, see Lessertisseur and Saban, 1967: 586). In some mammals (e.g., *Phascolarctos cinereus*) ossification never occurs and the atlas ring is completed ventrally by a ligamentous band.

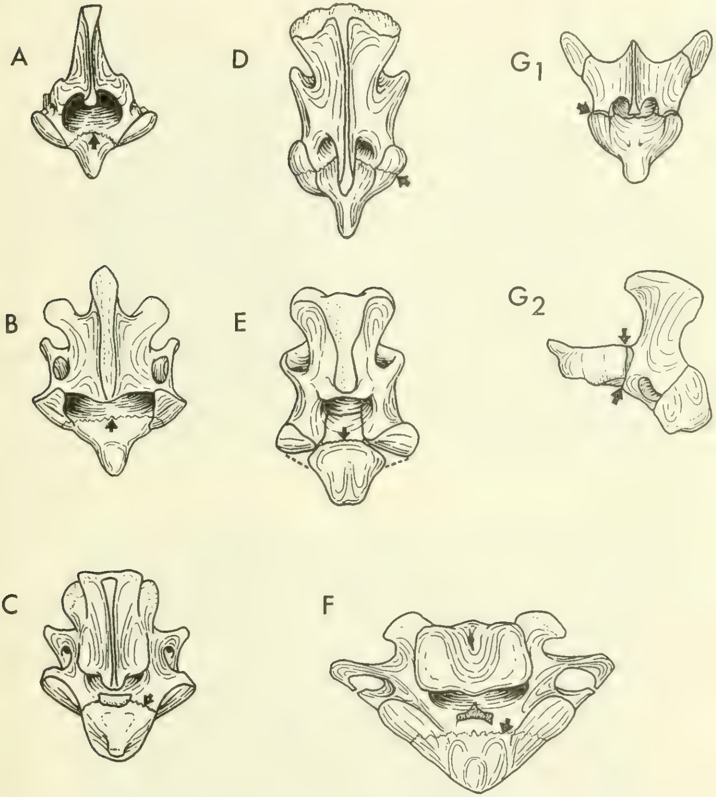

FIG. 8. Axes of juvenile mammals showing the joint (arrow) separating axial and atlantal centra. A, *Dasypus novemcinctus*, YPMOC 2333; B, *Sus scrofa*, YPMOC 1580; C, *Tapirus (Tapirella) bairdi*, YPMOC 287; D, *Canis familiaris*, YPMOC 2600, age 6 months; E, *Equus caballus*, YPMOC 198, age 12 days; F, *Elephas maximus*, YPMOC 210, age approx. 8 months; G_1 and G_2, *Tachyglossus aculeatus*, YPMOC 1691. All dorsal views, except G_2 which is lateral. Not to scale.

these facets approximately in half. In horses (Fig. 8E) and tapirs (Fig. 8C), the joint occurs in a relatively more anterior position, so that the greater part of the cranial articular facets are borne by the axis. The tendency to anterior displacement of the joint or, perhaps, posterior displacement of the facets is even greater in domestic pigs (Fig. 8B), while in some edentates (Fig. 8A) the joint passes entirely anterior to the facets. These examples are sufficient to show that in eutherians there is a considerable range of deviation in joint position from the primitive position posterior to the cranial facets. More importantly, however, these examples demonstrate that even in the most specialized forms the dens alone is not the sole vestige of the atlas centrum, as is generally believed. A postdens component always occurs. The retention of this component, even in those mammals in which the cranial articular facets are formed entirely from axis elements, relates not only to the phylogenetic history of the mammalian atlas centrum but also to the biomechanical function of the dens (to be considered in the next section).

Among previous workers, W. H. Flower was probably the first to recognize the actual dens-axis relationship. He reported (1885: 35-36) that "if the axis [of a mammal] is examined a year or two after birth, its body appears to be composed of two parts, one placed in front of the other, the first including the odontoid process [dens] and the anterior part of the body, the second all the remainder of the body." Flower drew no further conclusions from this observation, except to note that the posterior extremity of the odontoid ossification represented the "usual disk-like epiphyses of the vertebral bodies." Gadow (1933: 107) objected to these observations on the grounds that Flower "looked upon the odontoid as part of the axis centrum instead of a centrum in its own right. . . ." In fact, Flower did not reject the homology of the odontoid and atlas centrum, but implied, although somewhat indirectly, that more than just the odontoid process was homologous to the atlas centrum. Gadow and others err when they insist that the dens is a "centrum in its own right" that has become reduced in size and fused to the axis. This concept is untenable in view of both the paleontological and recent osteological evidence demonstrating that the dens arises from, and never completely replaces, the atlas centrum, and therefore is properly regarded as a neomorph. Yet authors usually cite unspecified "developmental evidence" to justify the supposed homology, despite the fact that some classical accounts of the subject (e.g., see Froriep, 1886) correctly portray the coexistence of both an atlas centrum and a dens during development. The interpretation of the developmental evidence has been a source of such confusion that it will be reevaluated here, using a marsupial as an example.

The development of the dens in the Virginia opossum, *Didelphis marsupialis*, has been studied with the use of serial sections and osteological preparations of pouch young. The critical question is whether the dens, at any time from its initial differentiation through its completed development, is an entity separate from the posterior ossification noted by Flower (1885) and here identified as the vestige of the atlas centrum. Separate development of the dens could possibly be construed as evidence of its homology with the primitive atlas centrum. Conversely, its development in association with a postdens component would support the paleontological and osteological evidence that it is not strictly homologous with the primitive atlas centrum.

The earliest section available is from a pouch young 20 days postpartum (Fig. 9A). At this stage the completely cartilaginous axis is characterized by two zones of hypertrophied chondrocytes (c_1, c_2). The dens (d) is recognizable as a bulbous excrescence on the anterior of the two zones. From the apex of the developing dens runs a connective tissue strand which later forms the apical ligament. The only feature which distinguishes the dens from the rest of the anterior zone is a slight indentation (*arrow*, Fig. 9A). Otherwise there is no indication at this stage that the dens is developing as an independent structure.

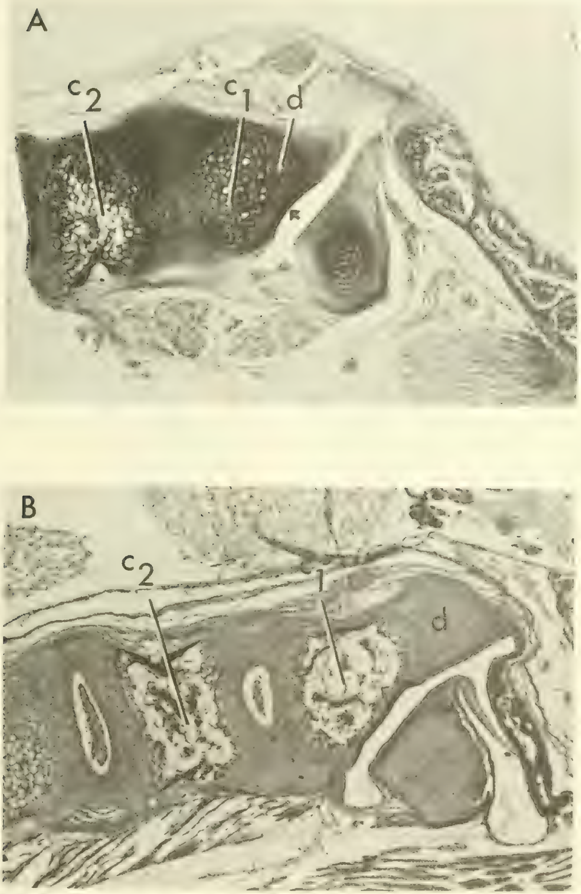

FIG. 9. Sagittal sections through the axes of opposum pouch young (*Didelphis marsupialis*). Upper photograph, 20 days post partum (Wistar Institute Ser. Cat. no. 17683), approx. X35. The two adjacent zones of hypertrophied chondrocytes represent the axis centrum (left) and "atlas centrum" (right). Arrow indicates developing dens. Below and to the right of the arrow is a section through the ventral half of the atlas ring ("atlas intercentrum"). Lower photograph, 25 days post partum, approx. X40. The two adjacent zones of ossification represent the axis centrum (left) and "atlas centrum" (right). The cartilaginous extension of the atlas centrum over the atlas ring represents the dens. For abbreviations see FIG. 1.

The second stage is from a pouch young of about 25 days postpartum (Fig. 9B). The ossifying axis centrum is clearly set off from the centrum of the third cervical vertebra and from an anterior ossification center by the developing intervertebral discs. The dens is still cartilaginous and is developing in conjunction with a large center of ossification (c_1) interpreted as serially homologous with the other ossifying centra. Parasagittal sections show that the dens is the apex of a broad-based, triangular mass of cells, of which the ossification center noted above forms the largest part.

The third and fourth stages are represented by osteological preparations of pouch young estimated to be 50 and 70 days postpartum. In the 50-day-old specimen (Fig. 10A), the axis consists of four unfused ossifications: the two neural arch halves, the axis centrum, and the "atlas centrum" with the dens. The "atlas centrum" (c_1, Fig. 10A) is a triangular ossicle, the blunt apex of which is directed anteriorly. The differentiation of the dens as a peglike, bony structure is just begun. In the 70-day-old specimen (Fig. 10B), the neural arches have nearly completed co-ossification. The axis is not yet ossified to the neural arches nor to the "atlas centrum" ossicle. The dens appears as a process arising from the "atlas centrum" ossicle of which it is a small part.

The fifth and last stage is represented by an osteological preparation of a young adult opossum estimated to be six months old (Fig. 10C). In this specimen the dens is but a small process arising from the "atlas centrum" ossification. This ossification, as in other marsupials, forms the anterior third of the axis body, to include the cranial articular facets. The joint between the "atlas centrum" ossification and the axis centrum is clearly visible.

The developmental history of the opossum dens demonstrates that the dens alone cannot be considered the homologue of the primitive atlas centrum, as is so often implied or stated. It is indisputable that the dens originates in conjunction with an embryonic structure, the so-called "atlas centrum" ossicle, which is homologous in position with the atlas centrum anlage of primitive tetrapods. Beyond this, it is useless to attempt to apply the concept of homology. The atlas centrum of mammals has been re-cast, so to speak, so that the dens is most appropriately regarded as a neomorph.

THE FUNCTION OF THE DENS

The functional importance of the dens is its adaptation to maintaining the integrity of the atlanto-axial joint. Most authors state that the dens acts as an "axis" or pivot about which the atlas rotates, but this function is of secondary importance. The atlas can and does rotate in the absence of a dens or in cases where the dens is congenitally separate from the axis. However, in such cases the joint is weakened and the possibility of atlanto-axial dislocation increased. The stabilizing function of the dens in the atlanto-axial joint is correlated with the loss of the atlanto-axial zygapophyses, which is necessary to permit rotation (see below, p. 41).

Rockwell, Evans and Pheasant (1938: 104) and Slijper (1946: 118) show that the basic mechanics involved in the suspension of the head and neck are those of a loaded beam that is supported at one end only. The centra may be considered as

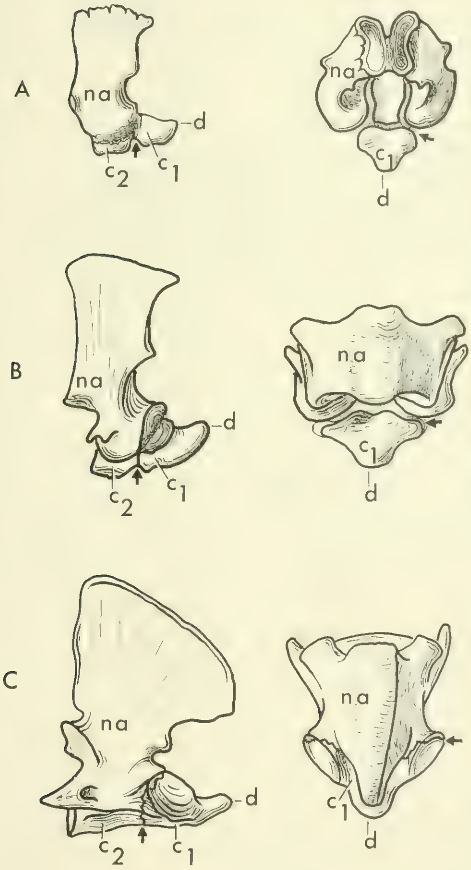

FIG. 10. The development of ossification of the axis in the opossum (*Didelphis marsupialis*). Left, lateral views; right, dorsal views. A, pouch young opossum, YPMOC 5502, estimated to be 50 days post partum. Approx. X5.25. B, pouch young opossum, YPMOC 5331, estimated to be 70 days post partum. Approx. X5.25. C, young adult opossum, YPMOC 243. Approx. X1.9. Arrow indicates joint between axial and atlantal centra. For abbreviations see FIG. 1.

compression-resisting members, and the neural arches, their processes, associated ligaments and muscles as tension-resisting members. With the loss of the atlanto-axial zygapophyses, this joint loses a critical tension-resisting mechanism. The weight of the head, which tends to flex the cervical series, therefore places a disproportionate amount of stress on the atlanto-axial joint relative to other cervical joints. To offset this structural weakness, several adaptations are possible. First, fusion of the atlas arches with the development of a dorsal atlanto-axial ligament replaces in some degree the lost zygapophyseal bond. But the ligament cannot be so extensive and taut that it interferes with the freedom of rotation; therefore, the ligament does not substitute for the zygapophyses, and the joint must be strengthened elsewhere.

A second possible adaptation is to increase the radius of curvature of the articulating atlanto-axial facets, resulting in a ball-and-socket joint. *Ornithorhynchus* (Fig. 7) shows the partial development of such a specialization. Yet this specialization is not common in mammals because it fails to balance completely the mechanical disadvantage engendered by the loss of zygapophyses. A ball-and-socket joint, in order to withstand the flexion stresses generated by the weight of the head, must be reinforced by strong ligaments along its dorsal margin. Such ligaments would also restrict the rotation of the joint, and hence nullify the rotational advantage gained by loss of the zygapophyses. In most mammals the atlanto-axial articulation is in fact shallow, with no indication of this type of specialization.

A third possible adaptation is to strengthen the atlanto-axial joint along its principal axis of movement, i.e., with a dens and its associated ligaments. These structures do not inhibit rotation because they reinforce the joint along the axis of rotation. The exceptions are the alar ligaments of the dens. However, these ligaments, which pass from the apex of the dens to the medial side of each condyle, are apparently important in the restriction of extreme rotational movement. (The other adaptations mentioned above reinforce the joint peripheral to its axis of rotation, and therefore tend to restrict rotation.) The functionally most important ligament with regard to the dens is the transverse ligament of the atlas (ligamentum transversum atlantis). This ligament passes from one side of the atlas arch to the other and divides the space for the dens below from the neural canal above. A synovial bursa between the dens and the transverse ligament facilitates rotation of the dens but does not interfere with the function of the ligament. This function, as generally recognized (Miller, et al., 1964: 103; Gray, H., 1959: 333), is to hold the dens against the ventral arch of the atlas. Acting together, however, the dens and transverse ligament prevent the atlas (and head) from flexing on the axis. The elongation of the dens and its retention by a transverse ligament anterior to the atlanto-axial facets is a simple mechanism for maintaining the strength of an intervertebral articulation without compromising rotational ability. The mammalian atlanto-axial joint without the dens and transverse ligament would be no less mechanically suited for rotation; it would lack, however, the mechanical means (musculature not considered) to sustain the stresses generated by the movements and particularly the weight of the head. The transverse ligament, as well as the apical and alar ligaments of the dens, maintains the integrity of a joint otherwise specialized to permit a very wide range of movement. In horses and in some ruminants (cow, sheep) the transverse ligament is negligible or absent (Barone and Lombard, 1967). However, in these forms functional replacements of the transverse ligament exist ("odontoid ligament"; "pseudo-alar ligaments") so that the mechanical role of the dens appears to be essentially unchanged.

Independent evolution of a dens and transverse ligament has apparently occured in birds. Possibly living reptiles have also independently evolved a dens or pseudo-dens complex. As Cuvier (1808) first observed, crocodiles typically have a short, median tubercle occupying a dorsal position on the anterior aspect of the dens, a position which Cuvier correctly noted was that of an odontoid process (true dens). Hoffstetter and Gasc (1969) figured atlas centra of certain lizards, snakes and amphisbaenids that likewise bear an anteriorly directed tubercle or eminence occupying a dens-like position; these authors, apparently ignoring this process, referred to the entire atlas centrum as the odontoid process. The studies of Gaupp (1908) and Williams (1959) revealed that the reptilian altas-axis joint possesses a number of bony and ligamentous similarities to the dens complex of mammals. To what extent the reptilian arrangement functionally parallels that in mammals is presently a moot point, but in no case should the terms odontoid process or dens be applied to the whole of the reptilian atlas centrum.

The Evolution of Atlanto-Axial Rotation

In pelycosaurs the possibility of atlanto-axial rotation is strictly limited by the nearly vertical zygapophyseal articulations (*pre z*, Fig. 6B) and by the posteriorly directed spine arising from the lateral surface of the atlantal postzygapophysis (*s a a*, Fig. 6A; see Romer and Price, 1940: 108). In cynodonts the zygapophyses of the axis are much reduced in size (*pre z*, Fig. 2A; see also the *Diademodon*(?) axis figured by Brink, 1955: 23) and the atlas postzygapophyses are altogether absent as distinct processes (see above). Therefore the possibility of rotation did exist, but it must have been limited because the articulating facets of the atlas neural arch and centrum are of approximately the same size. As a general rule, there is a disparity in the area of apposing facets when the joint permits a significant amount of sliding movement. In the atlanto-axial joint of the dog, for example, the axial facet extends dorsally beyond the atlantal facet on both sides. The extension allows continuous contact of articular cartilage as the atlas rotates.

Virchow (1914) demonstrated that one function of zygapophyses is to prevent intervertebral rotation. The evolution of the ability of the skull and atlas to rotate about the atlas centrum presupposes modification and eventual loss of the synovial joints of the atlanto-axial zygapophyses. In cynodonts the ventral aspect of the atlantal laminae lay across the dorsolateral surface of the vestigial axial prezygapophyses (Fig. 3B, C). Apparently the relationship between the two was analogous to a shelf (the atlantal laminae) supported by pegs (the vestigial axial prezygapophyses). However there are no distinct facets on the ventral surface of the laminae that would indicate the presence of a synovial capsule between the laminae and axial prezygapophyses. Therefore it is possible that the original synovial capsules were already replaced by a simple ligamentous connection. Whether the atlanto-axial "zygapophyseal" articulation in cynodonts was synovial or ligamentous, there is no question that this region is much modified from the primitive condition. The reduction and eventual loss of the primitive synovial capsule in this region is significant because of certain functional limitations that it imposed upon the joint. Zygapophyses are usually points of hinge-type movement; that is, the axis of movement is perpendicular to the facet surface at its center. Specialization (e.g., in crocodiles) often allows some sliding or gliding movement but such is probably limited to a relatively small excursion by the articular capsules which enclose them. Mammals, therefore, lose the atlanto-axial zygapophyseal articulation and specialize the atlanto-axial joint for rotation of the atlas neural arches and intercentrum about the atlas centrum. The supporting function of the lost zygapophyseal joints is replaced largely by the dens and its associated ligaments, by the ligamentum flavum and by the dorsal atlanto-axial ligament (e.g., in the dog, Miller, et al., 1964: 102, 104). Cynodonts represent an important phase in the transition to a mammalian atlanto-axial joint because the axial prezygapophyses no longer present any bony restriction to movement of the altantal arches.

The specialization of the mammalian atlanto-occipital and atlanto-axial joints is characterized by the tendency toward separation of the synovial capsules of one joint from the other. In cynodonts each half of the atlas neural arch bears two facets, one for the atlas centrum, the other for the occipital condyle (*f a c*, *f o c*, Fig. 1A). The two facets of a neural arch half are more or less confluent and are invariably covered by smooth, laminar bone. There is no evidence to indicate that these facets were divided by any sort of membrane. In all probability both facet surfaces were enclosed by a single "cervico-occipital" joint capsule. In this respect the cynodonts, despite their bicondylic condition, represent no advance over the pelycosaur condition. The separation of the "cervico-occipital" joint capsules into discrete atlanto-occipital and atlanto-axial capsules took place during a post-cynodont stage of evolution. This specialization is evidently related to a degree of joint movement which cynodonts had not yet achieved.

The second, or atlanto-axial, intervertebral foramen of most mammals is enlarged relative to other cervical intervertebral foramina. The evolution of atlanto-axial rotation apparently has necessitated this relative enlargement to prevent constriction of the second spinal nerve and associated vessels during normal movement. Spinal nerves and vessels caudal to the second cervical nerve are not subject to interference from the intervertebral foramina because the relative amount of movement between vertebrae is small. However the caudal intervertebral notch of the rotating atlas is considerably displaced relative to the cranial intervertebral notch of the axis. By offsetting the two halves of the atlanto-axial intervertebral foramen, rotary movement would damage the nerve and vessels if the foramen were not enlarged sufficiently to remain open despite rotation. Atlanto-axial rotation in living reptiles is apparently so slight that the nerve and vessels are not endangered; the atlanto-axial intervertebral foramen is comparable in size to those adjoining it. It is interesting that in pelycosaurs, which could not have had atlanto-axial rotation (see above), the atlanto-axial intervertebral foramen is comparable in size to others in the cervical series. Yet in cynodonts, where the reduction of the atlanto-axial zygapophyses allows the possibility of rotation, the atlanto-axial intervertebral foramen is markedly increased in size relative to other foramina (Fig. 3B). It is therefore likely that cynodonts did possess the ability to rotate the skull, atlas arches and intercentrum to some degree about the atlas centrum.

The ability of mammals to rotate the head and atlas about the dens of the axis is as much dependent upon specializations of musculature as it is upon specializations of joints and ligaments. Evans (1939: 54, 74–75) summarized the occipital and cervical musculature of representative reptiles and mammals. All three of the major systems of reptilian epaxial muscles—iliocostalis, longissimus, and transversospinalis—are also represented in the mammalian neck. The functional difference between the two classes probably lies in the greater amount of muscular specialization in mammals. This specialization may be manifested by regional differentiation, e.g., the semispinalis capitis into a biventer and complexus, or by partial reduction, e.g., the iliocostalis typically confined to the posterior cervicals. Nevertheless, both reptiles and mammals have evolved such a diversity of specializations that it is outside the scope of this work to attempt a thorough functional comparison. One major and consistent difference, however, occurs in the transversospinalis musculature between the occiput and atlas-axis and concerns rotation at the atlanto-occipital joint. In reptiles an M. obliquus capitis magnus originates on the axial spine and atlantal neural arch and inserts on the occiput; a small M. obliquus capitis minor[7] passes from the neural arch of the axis to the atlantal postzygapophyses (Evans, 1939: 54). In mammals these muscles are absent. In their place is an M. obliquus capitis cranialis (or superioris) passing from the wing of the atlas to the occiput and an M. obliquus capitis caudalis (or inferioris) originating on the spine of the axis and inserting onto the wing of the atlas. As an extensor of the atlanto-occipital joint, the obliquus capitis cranialis is a functional analogue of the reptilian obliquus capitis magnus. The obliquus capitis caudalis is primarily responsible for rotating the atlas and head about the dens of the axis and has no functional analogue of comparable efficiency in reptiles.

Distinct osteological modifications of the atlas and axis have evolved in conjunction with the mammalian obliquus muscles. Some of these are explicable in terms of increasing the efficiency of rotatory movement. One prerequisite of vertebral rotation is that the effecting muscle fibers must have a substantial transverse component in contrast to the typically longitudinal component of median epaxial muscles. In mammals this is accomplished by localization of rotational movement between two vertebrae, thus reducing to a minimum the longitudinal component of intervertebral muscles. The transverse component of these muscles is further increased by extending the atlas wing laterally and posteriorly, so that inserting fibers arising from the axis spine pass more directly laterally. Concomitantly, the length of the ossification representing the atlas centrum is reduced, with the result that the cranial articular facets of the axis impinge upon the joint which represents the union of the primitive atlantal and axial centra. Rotational efficiency is obviously increased by bringing the atlas ring as closely beneath and therefore lateral to the axis spine as is mechanically possible. The axis centrum of pelycosaurs and cynodonts, being of almost normal length, bears the atlas arch facets well ahead of the axis spine. This primitive condition is inherited by the monotremes. But in other mammals the same facets have migrated posteriorly; this displacement, together with the forward extension of the axis spine, results in an effective rotational component for the obliquus capitis caudalis.

In living reptiles (e.g., *Iguana, Sphenodon*), rotation probably occurs both at the atlanto-occipital and atlanto-axial joints, with the greatest amount of rotation at the former (see Evans, 1939). The prime movers in rotation are the Mm. obliquus capitus magnus and minor. In neither of these muscles is the lateral component as large as in mammals, i.e., with muscle fibers oriented at an angle of more than 45° away from the longitudinal spinal axis. The obliquus capitis magnus is the more oblique of the two, but its lateral component is reduced by virtue of passing some distance anteriorly over the atlas before inserting on the occiput.

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[7] Evans (1939) termed this muscle obliquus capitis inferior which duplicates the name of another muscle in mammals of entirely different attachment and function.

Before discussing atlanto-axial musculature in cynodonts, a critical evaluation must be made of the important contribution of Evans (1939) on the evolution of the atlas-axis from fish to mammals. In discussing cynodonts, Evans used *Galesaurus* and *Cynognathus* as prototypes; his conclusions were not based on original material, but rather on the descriptions of Parrington (1934) and Seeley (1895b). Evans (1939: 68) concluded that cynodont atlanto-axial "muscles, in keeping with the mammal-like character of the occiput, the atlas neural arch and transverse process, and the spinous process of the axis, were probably similar to those of a primitive animal such as the opossum." Evans' reconstruction (his fig. 11) of the muscles surrounding the atlas-axis of *Galesaurus* therefore shows the mammalian Mm. obliquus capitis cranialis and caudalis rather than the reptilian Mm. obliquus capitis magnus and minor. Evans' use of *Didelphis marsupialis* as a model for reconstructing cynodont occipital musculature is disputable on several grounds. First, the "mammal-like character" of the cynodont occiput to which Evans alluded does not necessarily indicate a mammalian arrangement of atlanto-axial musculature. I have examined several acid prepared galesaurid skulls and could find no muscle scars to support Evans' interpretation. Second, I cannot determine what features of the cynodont occiput that Evans recognized as exclusively mammalian. It is possible that Evans recognized a basic similarity in form and outline between the cynodont and generalized mammalian occiput, but these common characteristics are probably as much related to brain and jaw musculature requirements as occipital musculature. Occipital form is thus not solely determined by epaxial musculature. It is also possible that Evans interpreted the relative expansion of the cynodont occiput as similar to that in mammals; however, the occiput in pelycosaurs and even in cotylosaurs is a relatively broad surface and per se does not indicate a mammalian arrangement of musculature. In my opinion the cynodont occiput provides no evidence of a mammalian arrangement of atlanto-axial muscles.

Evans also claimed that the atlas neural arch and transverse process are mammal-like. The atlas neural arches, with the exception of the loss of postzygapophyses, are hardly more advanced than in pelycosaurs. The important step towards the mammalian condition—fusion of the laminae—has not occurred. As for the atlas transverse processes, Evans' figure shows them to be comparable in morphology and orientation to those of the third cervical vertebra. In fact the orientation of the atlas transverse processes, being nearly vertical, is different from that of the axis transverse processes (Fig. 3B). This feature is particularly difficult to account for in terms of a mammalian arrangement of musculature because in mammals the atlas wing tends to a more horizontal than vertical orientation. Therefore the cynodont transverse process is not prima facie evidence for a mammalian arrangement of obliquus muscles.

Finally, Evans cited the mammal-like character of the axis spine as evidence for his reconstruction of the muscles. However, it is difficult to define "the mammalian type" of axis spine in view of its wide range of morphological variation (see Lessertisseur and Saban, 1967: 607). In general, mammalian axial spines are elongate, flared laterally along their posterior margin, and bear a rather deep spinous fossa on the lateral surface. But the reptilian axis spinous process is also commonly elongate (Hoffstetter and Gasc, 1969) and comparable in shape to that in mammals. The common diminution or absence of a well-developed spinous fossa in the reptilian axis is correlated, in part, with the lack of expansion of the posterior margin of the spine. In cynodonts the spine is elongate (but little more so than in pelycosaurs; compare Figs. 2A and 6A); the spinous fossa is incipient; and the expansion of the posterior margin is negligible. There is no clearly defined aspect of the spinal morphology indicating that its associated obliquus muscles were of a mammalian arrangement.

Nowhere in Evans' analysis does there appear to be any cogent evidence for modeling a reconstruction of cynodont atlanto-axial musculature after a mammalian pattern. However, Evans (1939: 91) did outline how the arrangement of obliquus muscles of mammals might have been derived from the reptilian pattern. His theory is credible, but since it cannot be linked with any fossil evidence it is also purely speculative. The question of the exact disposition of obliquus muscles in cynodonts at present has no satisfactory solution, but it is a less important question once the functional aspects of the joint are recognized.

The significant aspects of cynodont anatomy with respect to atlanto-axial rotation are: 1) that the reduction of atlanto-axial zygapophyses removes any osteological obstruction to rotation; 2) that the orientation of the atlas transverse process is different from other cervical transverse processes, which is evidence for incipient specialization of the associated musculature, possibly for rotation; and 3) that the atlanto-axial intervertebral foramen is enlarged, a feature which is correlated in mammals with the prevention of spinal nerve and vessel occlusion during rotation. In these features cynodonts represent an advance over pelycosaurs in which the zygapophyses prohibit atlanto-axial rotation and in which the atlas transverse process and atlanto-axial intervertebral foramen are similar to others in the cervical series. Undoubtedly the atlas-axis relationship of cynodonts represents an initial phase in the evolution of a rotational joint. But in cynodonts it had obviously not attained the functional efficiency which has so narrowly canalized the morphology of this joint in mammals. Evans (1939: 68) erred when he compared the axis of *Cynognathus* with that of *Tachyglossus*, concluding that the atlanto-axial movements "chiefly abduction and a slight rotation"—were the same. Monotremes, in fact, have already achieved a mammalian type of specialization for rotation, including a well-developed dens and a typical atlas wing. In addition, they possess an ability of atlanto-axial abduction that probably was never developed in other mammals. This ability, as Evans notes, is due to the posterolateral extension of the axial facets for the atlas. It appears to be a specialization and perhaps is related to another specialization—the loss of all cervical zygapophyseal articulations. In cynodonts the ability to abduct could not have been very much developed because the apposing axis and atlas facets are of approximately the same size. In addition, the atlas laminae would have contacted the adjacent axis arch during abduction. The available evidence leads to the conclusion that atlanto-axial movement in cynodonts was restricted to a small amount of rotation.

Evolution of Atlanto-Occipital Flexion and Extension

The bicondylic atlanto-occipital joint of mammals is particularly specialized for flexion and extension. In *Didelphis*, for example, the flexion-extension arc is approximately 90°. In most, if not all, mammals the articulation also permits a small degree of abduction because the joint surfaces, viewed from above, represent arcs of a relatively large circle. Neither flexion-extension nor abduction at the atlanto-occipital joint are mammalian innovations, for both were undoubtedly present in synapsid and even in more primitive reptiles. The feature that characterizes the mammalian atlanto-occipital joint is the substantial increase in the flexion-extension arc. The starting point in its evolution is among pelycosaurs; they lacked any such specialization but reveal the basic plan from which it was developed. The mammalian specialization that permit the extensive range of movements will be defined before cynodont anatomy is evaluated as a stage in their development.

The phylogenetic history of the mammalian atlanto-axial joint has demonstrated the principle that specializations for greater freedom of movement evolve concomitantly with specializations for increased control and for maintaining the strength of the joint. In the pelycosaurian atlanto-occipital joint the joint surfaces (excluding the proatlas) are in size comparable to the intercentral articulations of postaxis vertebrae. In terms of structural elements the atlanto-occipital joint represents a slightly modified intercentral articulation. The joint itself is rather shallow (Fig. 11A), a feature which undoubtedly permitted a certain amount of freedom but which could not contribute to its strength. Thus the pelycosaurian atlanto-occipital joint sacrifices some strength for mobility and the inherent weakness must be compensated for elsewhere. The critical stresses at the atlanto-occipital joint are produced by the weight of the head. The forces generated, as noted before (p. 38), are those of compression along the ventral half of the spinal column, i.e., between centra, and tension along the dorsal half, i.e., between neural arches and zygapophyses. A shallow atlanto-occipital joint may adequately accommodate compressive forces between the condyle and the atlas, but it is not suited to resist tensile forces, i.e., the tendency to atlanto-occipital flexion or separation induced by the weight of the head. Hence an additional element is required—the proatlas—analogous in function to the zygapophyses of other cervical vertebrae. The important functional difference between cervical zygapophyses and the proatlas is that the former have only one joint capsule to a side whereas the latter, articulating with both the atlas neural arch and occiput, has two. The proatlas ossification provides a tension-resisting element, while the fact that it has two joint capsules allows more latitude for movement than would be possible at one capsule. Nevertheless the proatlas essentially restricts both flexion and extension.

In mammals the proatlas is absent or, rather, does not ossify separately. The ventral half of the "pro-atlantal" sclerotomite forms the apex of the dens (see below). The dorsal half, which in certain reptiles ossifies as the proatlas, apparently has a variable role in mammalian development. Hayek (1923; 1927: 276–278) claimed that in man, moles, rabbits and other mammals the proatlas arch anlage contributes to the formation of the occipital condyles, an observation which has been repeated for

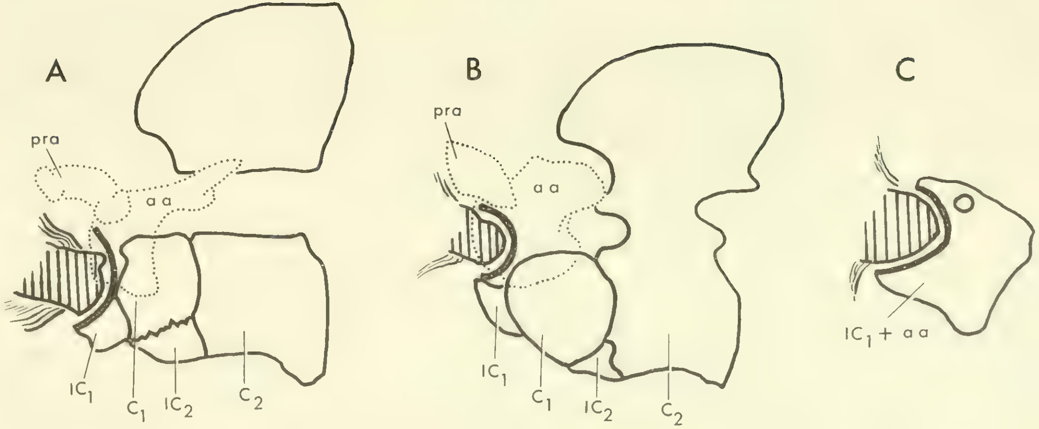


FIG. 11. A, reconstructed sagittal section through the atlanto-occipital joint of a pelycosaur. The same for B, a cynodont, and C, a dog, except that these sections are parasagittal because the condyles are located lateral to the sagittal plane. Heavy line indicates the relative depths of the atlanto-occipital joints. Dotted line traces the outline of the atlas, neural arch, and proatlas in the pelycosaur and cynodont. Not to scale.

human embryos more recently by Ingelmark (1947) and Sensenig (1957). The latter author also claimed that the proatlas arch contributes to the formation of alar and other ligaments of the atlanto-occipital joint. However, Barge (1918) found that in sheep the neural arch half of the "pro-atlantal" sclerotomite joins with the atlas and Sensenig (1943: 133) confirmed the same condition in *Peromyscus*. Apparently the lack of separate ossification of the proatlas in mammals permits its anlage to follow a variety of developmental courses.

The absence of a proatlas in mammals is probably correlated with the increase in the flexion-extension arc. However the loss of the proatlas alone does not account for the substantial increase in the flexion-extension arc. Since the proatlas primarily strengthens the atlanto-occipital joint, its loss requires compensatory adaptations which will maintain the strength of the joint and at the same time permit considerable latitude in flexion and extension. The two most important adaptations are therefore interrelated: the doubling of the condyles and the decrease in their radius of curvature. Doubling the condyles provides potentially a greater amount of articular surface and, hence, strength to the joint. However a large, broadly curved articular surface as in pelycosaurs is an inefficient hinge for flexion and extension. Such a surface engenders more displacement of the occiput per degree of flexion than a sharply curved surface. The mammalian double condyle provides both the larger area of articular surface for a stronger joint and the smaller radius of condylar curvature to facilitate flexion-extension (Fig. 11C). In addition, the dorsal margins of the occipital facets of the atlas are commonly reflected ventrally (Lessertisseur and Saban, 1967: 602), thus extending the facet surface and at the same time tending to encircle the condyles. The condyles themselves become hemicylindrical and, more importantly, their ventral surfaces are extended anteromedially to provide facet area for maximum flexion. Furthermore the development of lateral atlanto-occipital ligaments (e.g., in the dog, see Miller, et al., 1964: 101; or in the horse, see Sisson and Grossman, 1953: 217) reinforces the joint yet does not interfere with flexion or extension because these ligaments approximately coincide with the transverse axis of movement. The mammalian atlanto-axial joint thus combines features that permit an increased degree of flexion and extension but that also are adapted to transmitting the stresses of head weight.

The cynodont atlanto-occipital joint shows significant advances over the pelycosaurian condition with regard to increasing the flexion-extension arc (Fig. 11B). Most cynodonts are truly biocondylic and have eliminated the possibility of atlanto-occipital rotation present in pelycosaurs. In this sense, cynodonts have begun to specialize the joint for flexion and extension; by doubling the condyles the relative amount of articular surface is increased and the radius of condylar curvature is also increased. The anterior neural arch facet for the occipital condyle is anteroposteriorly longer than the adjoining facet for the atlas centrum, which is the reverse of the pelycosaurian condition. Nevertheless the atlantal facets for the occipital condyles are still comparatively shallow. The articular cartilage of the atlas, supported by three independent elements, intercentrum, neural arch and centrum, could not form as strong an articular capsule as in the mammalian atlas where these elements are fused. Extension was almost centainly limited by the intercalation of the proatlas between arch and occiput. The proatlas also probably restricted flexion; the lack of any significant ventral extension of the condylar facets is corroborative evidence. The possibility that cynodonts possessed a greater flexion-extension arc than pelycosaurs appears likely on evidence of the doubling of condyles. Nevertheless cynodonts retained many features of a pelycosaurian grade and lacked the mechanical refinements which are so characteristic of the mammalian arrangement.

3. THE POSTCRANIAL AXIAL SKELETON OF *THRINAXODON*

MATERIAL. A nearly complete, articulated axial skeleton of *Thrinaxodon* cf. *liorhinus* (AMMM 5265) is described below. The matrix was removed by acid, revealing most of the minute details. The specimen is for the most part undistorted. Missing are most of the cervical ribs, the distal ends of most thoracic ribs, and the caudal vertebrae. The atlas-axis complex is incomplete and damaged, but this is well known from other specimens. Other small breaks in the neural spines and costal plates aside, this specimen as preserved represents the most perfect of known cynodont axial skeletons.

Numerous other *Thrinaxodon* axial skeletons, most of them incomplete, damaged during preparation, or incompletely prepared, were studied as additional reference material. Among the more important of these specimens are those in the National Museum (Bloemfontein, Republic of South Africa) collection, originally described by Brink (1954). Others include AMNH 2228, USNM 22812, BPI 287 and BPI 376. However, unless otherwise specifically cited by number, the following description is based on AMMM 5265.

CERVICAL SERIES

MORPHOLOGY. The number of cervical vertebrae in *Thrinaxodon* is of interest to compare with the almost invariable mammalian number of seven. The determination of the number is complicated by the fact that *Thrinaxodon*, unlike most mammals, retained cervical ribs, the absence of which is a primary feature of mammalian cervical vertebrae. Brink (1954: 117) described *Thrinaxodon liorhinus* (NMB C.392) as having five cervical vertebrae. Brink's division between the cervical and thoracic series was based apparently on his observation that the "first thoracic vertebrae [*sic*] has the tallest dorsal process." Re-examination of this specimen shows that in fact the heights of the neural spines on the fifth, sixth and seventh vertebrae are subequal and that the state of preparation prohibits a confident estimate as to which, if any one, is the highest. Two acid-prepared specimens of *Thrinaxodon* (SAM R.377, SAM uncatalogued), if considered together, show that the spine of the seventh vertebra is slightly taller than any preceding spine. Brink (1954: fig. 2) restored the seventh and eighth neural spine of *Thrinaxodon* as the tallest, which is probably correct. A clearly defined morphological division is evident in AMMM 5265 between the seventh and eighth vertebrae; as will be documented more fully below, this transition involves a shift in orientation of the zygapophyses and transverse processes and a change in the morphology of the neural spines. The same morphological changes are consistently developed in other specimens and therefore I conclude that *Thrinaxodon* has seven and not five cervical vertebrae.

Intercentra occur as single, crescentic ossicles interposed ventrally between successive pleurocentra; their width is approximately one half the width of the adjacent pleurocentra. In AMMM 5265, intercentra are preserved between the first five centra (IC_1, IC_2, etc., Fig. 12B, C); from the appearance of the beveling along the adjacent ventral margins of the fifth, sixth and seventh cervical vertebrae, intercentra probably occurred here also. An intercentrum possibly occurred between the last cervical and first thoracic, but caudal to this point intercentra are certainly absent.

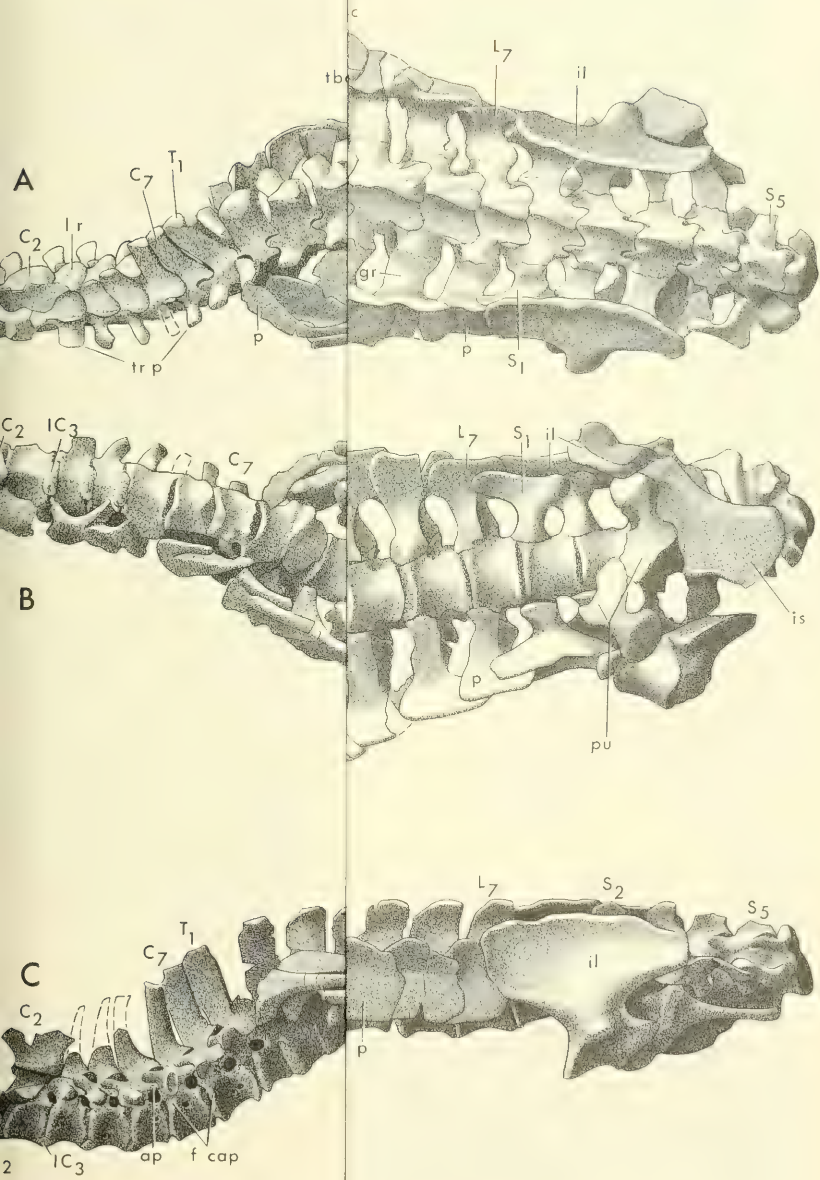
Pleurocentra are deeply amphicoelous, approximately circular in cross-section and slightly constricted laterally and ventrally around the middle. Facets for the rib head occur as clefts between adjacent centra; each cleft is formed by two opposed facets obliquely beveled into the dorsolateral aspect of the rims of adjacent centra (*f cap*, Figs. 12C, 13A).

Pedicles join the body along an irregular suture. Anteriorly, each pedicle forms a protruding lip which overhangs the rim of the centrum and thus participates in the intervertebral articulation; functionally, the protruding pedicle lips may have served to inhibit dorsal displacement of an anterior relative to a posterior vertebra. The pedicles are indented anteriorly and posteriorly to form cranial and caudal vertebral notches of which the former is invariably the most deeply incised. The intervertebral foramen thus formed is bordered dorsally by a posteriorly directed anapophysis received into a lateral depression of the next posterior pedicle (*ap*, Figs. 3B, 12C). This lateral depression occurs directly dorsal to the cranial vertebral notch and lies directly ventral to the prezygapophysis.

Anapophyses arise ventrolaterally to the postzygapophyses as elongate, blunt eminences which are smoothly convex laterally but which are flattened medially to conform with the lateral depression of the following pedicle. Anapophyses diminish in size anteriorly and do not occur on the atlas.

The pedicles bear stout transverse processes, diapophyses, which are directed posterolaterally and ventrally on the axis and on the third through the sixth cervical vertebrae (*tr p*, Figs. 3, 12). The transverse processes of the seventh cervical are the most slender and project laterally; on the first thoracic vertebra, they project anterolaterally. The facets for the tuberculum also show a morphological gradient. On the axis the facet is an elongate oval, the long axis of which is directed anteroventrally ($tr\ p_2$, Fig. 3A–C; in Fig. 12C, the left half of the axis arch is lost; in Fig. 12B, the right transverse process is obscured by its rib). On the posterior cervicals the facet becomes successively less elongate and its long axis more vertically oriented, so that at C_7 the facet is nearly round with a slight ventral projection from its anteroventral corner. This projection becomes successively more developed in the thoracic series until the tubercular and capitular facets are continuous and form a synapophysis.

The angle of zygapophyseal articulation increases from an angle of approximately 45° to the horizontal between the axis and third cervical vertebra to an angle of about 55° between the sixth and seventh cervical vertebrae. The laminae that bear the zygapophyses decrease in breadth from 7.3 mm on the axis to 5.8 mm on the seventh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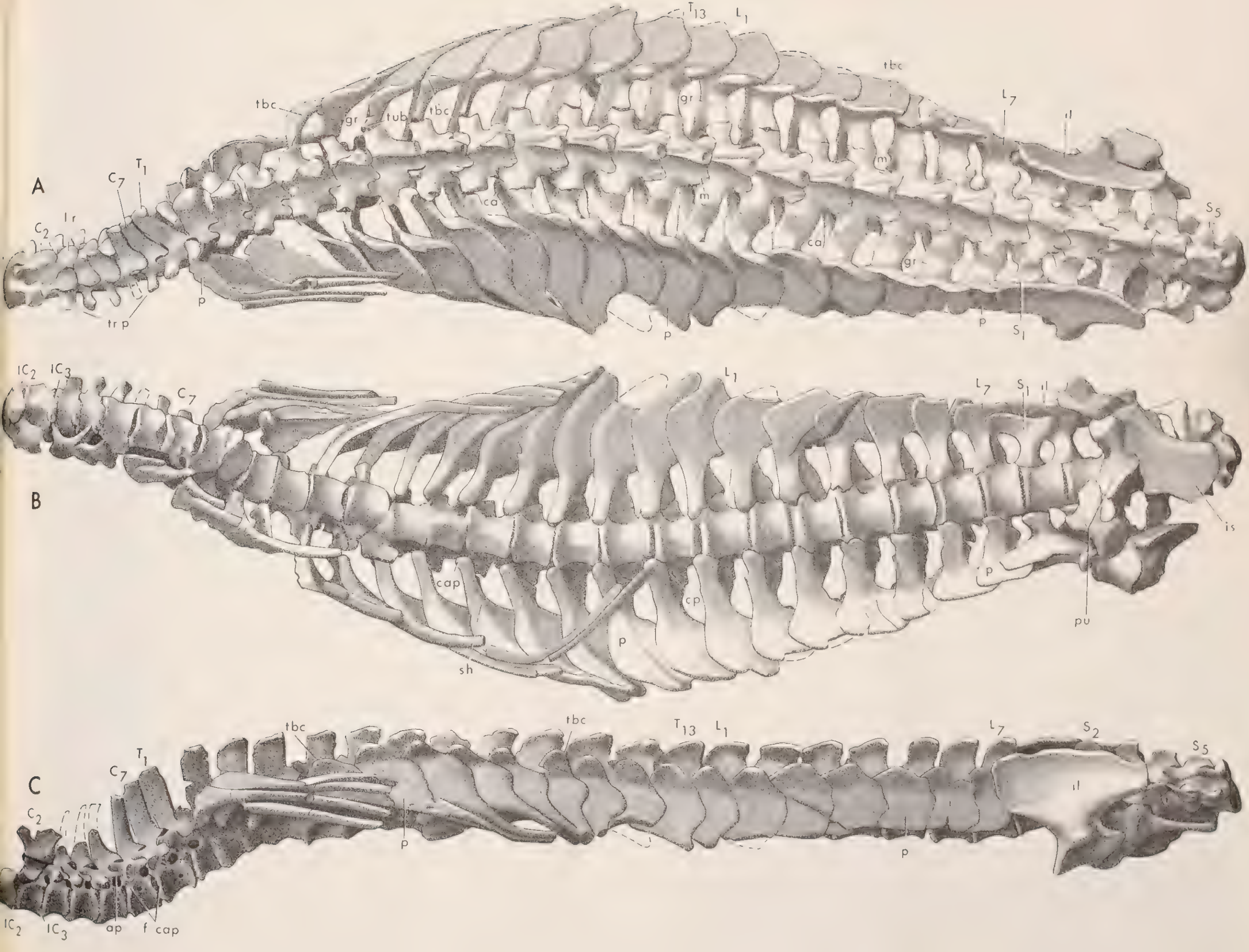

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FIG. 12. The postcranial axial skeleton of *Thrinaxodon* sp., AMMM 5265. A, dorsal; B, ventral; C, lateral views. Dashed lines represent areas reconstructed from other specimens. X1.5. Abbreviations: *ap*, anapophysis; C_1, C_2, etc., first cervical, second cervical, etc.; *ca*, concavity between anterior aspects of capitulum and tuberculum; *cap*, capitulum; *cp*, concavity between posterior aspects of capitulum and tuberculum; *f cap*, facets for capitulum; *gr*, groove between costal tubercle and tuberculum, probably for the ilocostalis muscle; IC_2, IC_3, second and third intercentra; *il*, ilium; *is*, ischium; L_1, L_2, etc., first lumbar, second lumbar, etc.; *l r*, ridge on lamina; *m*, metapophysis; *p*, costal plate; *pu*, pubis; S_1, S_2, etc., first sacral, second sacral, etc.; *sh*, rib shaft; *tbc*, costal tubercle on rib plate; *tr p*, transverse process; *tub*, tuberculum. (see inside)

FIG. 1
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shaft;

cervical vertebra, measured between postzygapophyseal extremities. This decrease continues through the fifth cervical, but from the sixth cervical posteriorly there is a gradual increase in this dimension.

A very slight ridge runs anteroposteriorly across the dorsal surface of the laminae of the third through the seventh cervical vertebrae (*l r*, Figs. 3C, 12A). The ridges on the third cervical, barely discernable, bisect each lamina between the base of the spine and the lateral edge of the postzygapophysis. On posterior cervical vertebrae the ridge becomes successively closer to the postzygapophyseal edge because of the narrowing of the laminae and on the seventh cervical it forms the lateral edge of the postzygapophysis. Typically the lateral surface of the pedicles directly ventral to the transverse processes and the ventrolateral sides of the centra are fenestrated by large nutrient canals.

The neural spines are tall, narrow and slightly recurved caudally; the spines on the third through fifth cervical vertebrae show a gradual but distinct anteroposterior tapering toward the apex of the spine (Fig. 12C) that is less developed in the sixth and seventh cervicals. In cross-section cervical spines are elliptical, but on the seventh cervical the posterior margin is swollen in conjunction with the transition to the triangular cross-section found in thoracic spines. The eighth vertebra, i.e., the first thoracic, bears a spine that is distinctly triangular in cross-section and is thus differentiated from all cervical spines.

Thoracic Series

MORPHOLOGY. The morphological transition between the cervical and thoracic series is gradual and not extensive. Intercentra are absent in all postcervical vertebrae, with the possible exception, noted above, of an intercentrum between the seventh cervical and first thoracic vertebrae. Thoracic pleurocentra increase caudally in length and width (Fig. 12B), but this change is slight and they are otherwise morphologically identical to the cervical pleurocentra.

The abrupt change in zygapophyseal orientation is the only definite marker separating thoracic from cervical vertebrae. The facets of the prezygapophyses on the seventh cervical vertebra have an orientation of approximately 55° to the sagittal plane, similar to the facet orientation in the cervical series. On the same vertebra, the articular facets of the postzygapophyses lie within approximately 15° of the sagittal plane, i.e., nearly vertical. The remaining thoracic articulations also appear to be at a similarly high angle, although there is a tendency in the more posterior thoracics to slightly more horizontal orientation, estimated at 20 to 25° from the sagittal plane. A more complete account of the nature of articular facet orientation is given below (see p. 64) for *Galesaurus*. The fact that this specimen of *Thrinaxodon* (AMMM 5265) is articulated prevents more detailed observations.

The increase in length of thoracic vertebrae may be expressed in terms of the distance between the anterior end of the prezygapophysis and the posterior end of the postzygapophysis of a given vertebra. On the first thoracic of AMMM 5265, for example, the length is 7.3 mm; on the sixth, 8.6 mm and on the 13th thoracic, 10.5 mm. Lumbar vertebrae increase only slightly in this dimension.

The transverse processes of anterior thoracic vertebrae do not extend as far laterally as they do in the cervical series. On the fifth cervical vertebra the transverse distance between the lateral margins of the transverse processes is 13.2 mm; on the seventh cervical, where the processes project directly laterad, the distance is 14.0 mm. In contrast, the same measurement on the first thoracic vertebra is 12.9 mm, and on the sixth thoracic it is 11.5 mm. Thereafter, however, the lateral extension of the transverse processes increases; so that at the seventh thoracic vertebra it measures about 12.2 mm (slight damage here introduces uncertainty) and at the 13th and last thoracic vertebra, it is 13.6 mm.

The ribs of the anterior thoracic vertebrae in AMMM 5265 are partially dislodged and the transverse process facets thus exposed show the beginning of a morphological gradient which, in the lumbar series, culminates in confluence of the tubercular and capitular facets. The gradient begins at the first thoracic vertebra, the transverse process of which has a slight anteroventral extension in the direction of the facet for the capitulum. This feature is fully described below, p. 63, from a galesaurid in which all of the thoracic ribs are missing on one side.

The transverse processes also exhibit a progressive displacement throughout the thoracic and into the lumbar series. On the first through the third thoracic vertebrae, the transverse processes arise from the anterior half of the pedicles, and are ventral and slightly posterior to the prezygapophyses. In posterior thoracics the processes become broader anteroposteriorly and at the same time progressively shift posteriorly, i.e., arising from the pedicles at points more nearly equidistant from pre- and postzygapophyses.

The height of the neural spines gradually diminishes from the posterior cervicals, estimated at 9 mm through the seventh thoracic vertebra, approximately 5.5 mm, and thereafter the height decreases only slightly, < 1 mm. From the first through the 13th thoracic vertebrae, the neural spines increase in anteroposterior length, being 3.7 mm on the first thoracic and about 7 mm on the 13th. In cross-section thoracic neural spines are triangular with an expanded, vertical posterior face and two lateral faces converging anteriorly as a thin blade. The anterior margin of the blade, beginning at about the fifth thoracic, is enveloped by a vertical cleft in the posterior margin of the preceding neural spine. Concomitantly the base of the neural spine increases in transverse breadth, particularly across the posterior half of the spinal base. The total increase is on the order of .75 mm and occurs between the first thoracic and the fifth or sixth thoracic vertebrae. Thereafter this dimension remains relatively constant even into the lumbar series. The spinal apices terminate by a rugose tuberosity which bears a shallow depression on the posterior dorsal surface (Fig. 12A). The rim of the depression is defined by a narrow lip of compact bone, but the bottom is floored by spongy bone, often with visible trabeculae. The transition between rim and depression floor is abrupt, as if the compact bone had been removed post-mortem. However the depression is preserved on most vertebrae and in dorsal view shows a distinct morphological gradient from anterior to posterior vertebrae, proving that the feature is not an artifact of preservation. On anterior thoracic vertebrae the lateral edges of the depression are extended and attenuated anteriorly to create a crescent-shaped depression. At approximately the eighth cervical vertebra, the anterolateral edges are reduced and the depression outline assumes an hourglass shape, being somewhat constricted at the sagittal plane. The depression, identifiable on most thoracic and lumbar vertebrae but absent in the cervical, sacral and caudal series, probably represents the attachment of a supraspinous ligament.

Lumbar Series

MORPHOLOGY. There are seven lumbar vertebrae in *Thrinaxodon*. Lumbar vertebrae differ from thoracic by a slight increase in centrum width, by the development of robust transverse processes, and by the union of parapophysis and diapophysis to form a synapophysis. However the distinction between the lumbar and thoracic series is based on the rib morphology in the posterior dorsal vertebrae. The first lumbar vertebra is designated as the first dorsal vertebra lacking a rib shaft distal to the costal plate of its associated rib. As rib morphology is also gradational, the selection of the first lumbar vertebra is somewhat arbitrary. Nevertheless there is no doubt that the thoracic and lumbar series are sufficiently distinct to warrant separate recognition, despite the fact that they are morphologically intergradational.

The progressive increase posteriorly in centrum width is a continuation of a trend begun in the thoracic series; measured along a transverse line dividing the centrum into equal anterior and posterior halves, the first lumbar centrum is 6.5 mm and the seventh lumbar centrum is 8 mm wide.

The development of more robust transverse processes is also a continuation of a trend begun in the thoracic series. Anteroposteriorly the lumbar processes are broader than in the thoracic series and they are dorsoventrally deeper as well. From the fifth to the seventh lumbar vertebrae the capitular facet (parapophysis) is located on the respective centra only, whereas in the first to fourth lumbar vertebrae the facet is shared by adjacent centra.

The transverse breadth between extremities of the postzygapophyses increases posteriorly, a continuation of the trend begun at the sixth thoracic vertebra; on the first lumbar vertebra in AMMM 5265, for example, the breadth is 7.7 mm, while on the sixth, it is 8.5 mm. An exception is the seventh vertebra which becomes narrower in this dimension, approximately 7.2 mm, in conjunction with the transition to the sacral series.

The length of the anterior lumbar vertebrae, measured between zygapophyses, is 11.1 mm and represents an increase over posterior thoracic vertebrae of about 0.5 mm. The posterior lumbars are equal in this dimension, again with the exception of the seventh lumbar vertebra which, at 9.5 mm, is approximately 1.5 mm shorter than those of the posterior lumbars.

Sacral Series

MORPHOLOGY. The sacral vertebrae are defined on the basis of their rib contact with the medial surface of the iliac blade. The caudal margin of costal plate of the seventh lumbar rib contacts the cranial margin of the iliac blade but in form and function this vertebra unquestionably belongs to the lumbar series. The sacrum, thus defined, is composed of five vertebrae, not four as claimed by Brink (1954: 119). The specimens available to Brink apparently did not show the fifth sacral rib contact with the ilium, and thus the fifth sacral was mistaken for the first caudal. The posterior margins of the ilium have been lost in AMMM 5265 and therefore it is difficult to be certain about the sacro-caudal division in this specimen. However in two other specimens of *Thrinaxodon* (AMNH 2228, NMB C.143), the sacroiliac articulation is sufficiently preserved to establish definitely five vertebrae in the sacrum. The fifth sacral vertebra lies almost entirely behind the posterior extremity of the iliac blade; the sacroiliac contact is made in this case by a slender, anteroventrally directed process of the fifth sacral rib.

The sacral centra are similar in morphology and dimensions to those of the lumbar series. In AMMM 5265 the distance between the lateral edges of the prezygapophyseal facets of the first sacral vertebra (7.2 mm) is comparable to those of the posterior lumbar series (8.2 mm), but the distance between the lateral edge of the postzygapophyseal facets of the same vertebra is reduced by almost one half (4 mm). On the second sacral vertebra the distance between the lateral edges of the postzygapophyses decreases to 3.7 mm, but thereafter successively increases on the third through fifth sacral vertebrae; on the last it measures 5.3 mm. The zygapophyseal facets articulate at extremely high angles, i.e., nearly parallel to the parasagittal plane, and the zygapophyses are much smaller than lumbar zygapophyses. There are anapophyses, as in the lumbar series, but they are smaller.

The short, stout transverse processes of the first sacral vertebra are less robust but otherwise very similar to those of the seventh lumbar. Sacral transverse processes posterior to the first sacral vertebra are successively more slender.

The sacral neural spines are less elongate anteroposteriorly than those of the lumbar series and their apices lack the tuberosities and depressions characteristic of the dorsal vertebrae. The spines of the fourth and fifth sacral vertebrae are essentially like those of the caudal series, being short and having a more or less oval apex.

Caudal Series

MORPHOLOGY. Broom (1932b: fig. 41) gave a reconstruction of *Thrinaxodon liorhinus* with 16 caudal vertebrae, assuming a sacral count of four. Broom made no mention of how he determined this number nor did he describe the specimen on which he based his reconstruction. Describing cynodonts in general, Broom (1932b: 263) wrote that there were "a small number of caudals perhaps twelve to twenty." Brink (1954: 119, fig. 2) followed Broom, illustrating 16 caudal vertebrae. But Brink believed the sacrum contained only four vertebrae, whereas it has been shown (see foregoing section on sacral vertebrae) that Brink's first caudal contacts the ilium and is actually the fifth sacral. Hence in Broom's and Brink's reconstructions there are 15 caudal vertebrae, not 16.

The actual number of caudal vertebrae in *Thrinaxodon*—or in any cynodont—is in doubt because available specimens are incomplete. In NMB C.392 there are only five and one-half caudals and in NMB C.142 there are three; both specimens are incompletely prepared and in damaged condition. In AMNH 2228, four caudal vertebrae and part of the fifth are preserved and have been acid prepared. This last specimen is the only material from which an accurate description of cynodont caudal morphology can be made.

In AMNH 2228 the neural spines decrease in height from the first caudal (4 mm) to the third caudal vertebra (2.5 mm). The neural spine of the fourth caudal is missing. The spines are less elongate anteroposteriorly than in the sacral series, and their apices are oval.

The zygapophyseal articulations between the fifth sacral and first caudal and between the first two caudal vertebrae appear to be nearly vertical in dorsal view, much as in the sacral series. The articulations between the second and third and between the third and fourth caudal vertebrae are more oblique but are within 20° of the parasagittal plane. However the third and fourth caudals have been partially disarticulated and show that the nearly vertical facet of each prezygapophysis turns medially and horizontally at the base of the prezygapophysis. Thus each prezygapophysis is half of a cup-shaped depression. Postzygapophyses likewise bear a vertical facet area laterally and a horizontal facet area medially. This feature will be described in more detail below with reference to thoracic vertebrae in *Galesaurus.*

Anapophyses are present, but are much smaller than in the sacral or pre-sacral series.

Transverse processes are robust and very short. They are directed posterolaterally and ventrally, whereas sacral transverse processes are directed more or less laterally. Since a separate capitulum is not developed on caudal ribs, the transverse process is the sole structure joining caudal ribs and vertebrae. In AMNH 2228 the transverse process-rib articulation appears to have been at least partly ossified.

It is possible that there were less than 15 or 16 caudal vertebrae in *Thrinaxodon* judging by the rapid diminution of vertebra size. The length of the second caudal in AMNH 2228 is 5 mm, while the fifth caudals is 4 mm, compared to a length of 7.3 mm at the first lumbar. On the basis of available material, I would estimate a caudal count of 10 to 15.

Broom (1932b: fig. 92) and later Brink (1954: fig. 2) reconstructed *Thirnaxodon* as having chevron bones, or haemapophyses, associated with most of the caudal vertebrae. There is no substantial evidence of these in AMNH 2228 other than a few unidentifiable bone scraps which are probably broken pieces of ribs or vertebrae. There is thus considerable doubt that *Thrinaxodon* possessed caudal chevrons.

Ribs

Ribs are associated with all cervical, thoracic, lumbar and sacral vertebrae. All caudal vertebrae, insofar as known, also possess ribs.

Cervical Ribs

MORPHOLOGY. In AMMM 5265, the proximal ends of several cervical ribs are preserved on the right side. Their damaged condition limits description to the following observations. In lateral view a typical proximal rib end is a small, triangular plate; the apex of the triangle is continuous with the (broken off) rib shaft, while the base lies against the vertebra. This triangular expansion for the most part represents the diverging capitulum and tuberculum, which are not separated as distinct processes. The dorsal margin of this triangular expansion bears a narrow, vertical flange which represents a small cervical costal plate. Cervical ribs were probably directed posterolaterally as well as ventrally. There could have been little, if any, overlap between the platelike proximal ends of adjacent ribs because they were probably oriented more or less vertically. Nothing can be described of the shape and orientation of the capituli and tuberculi nor of the length of cervical ribs.

Thoracic Ribs

MORPHOLOGY. No sharp morphological discontinuity occurs between the cervical and thoracic ribs, although the two rib types in the middle of each series are well differentiated. The ribs of the sixth cervical to third thoracic vertebrae are of intermediate morphology.

The capitulum of thoracic ribs is a stout process which, like that of the cervical ribs, is continuous with the distal shaft of the rib by a ridge along the ventral aspect of the costal plate (*cap*, *sh*, Fig. 12B). The capitulum and tuberculum (*tub*, Fig. 12A) of the anterior thoracic ribs lie relatively close together; the capitulum is ventral and slightly anterior to the tuberculum and directed medioventrally and slightly anteriorly. This condition approximates that found in the cervical series. In the posterior thoracics beginning at the seventh or eighth thoracic, the capitulum progressively shifts its orientation anteriorly so that the angle formed between the posterior edge of the capitular process and the vertebral column decreases from approximately 85° at the fifth thoracic to 70° at the tenth thoracic (Fig. 12B). Thereafter the trend is reversed and the capituli become directed more medially and less anteriorly; at the first lumbar the capitular process forms a 90° angle with the vertebral column.

In the posterior thoracics the capitulum becomes progressively more elongate until, at the 13th thoracic, it extends almost to the level of the ventral surfaces of the centra. The capitulum also becomes increasingly robust, a trend which culminates in the confluence of capituli and tuberculi in the lumbar ribs. Thoracic ribs are not fused to the transverse processes as are the lumbar ribs, although the ribs of the 12th and 13th thoracic vertebrae appear to have a serrate suture and the joint may have had reduced mobility.

The tuberculi of thoracic ribs are short, stout processes, each separated from the associated capitulum ventrally by a thin lamina of bone. As stated previously, the tuberculi of the anterior thoracics lie above and slightly behind the capituli, and therefore the bony laminae between them are oriented almost vertically. In the posterior thoracics the transverse processes broaden anteroposteriorly and the tuberculi likewise broaden.

In the anterior thoracics the anterior surfaces of the laminae between capituli and tuberculi are flat. Posterior to the seventh thoracic rib these surfaces become successively more concave. Concomitantly an anteriorly reflected lip develops on the anterior margin of each capitular process, and consequently the area between each capitulum and tuberculum becomes a broad concavity (*ca*, Fig. 12A). The opposite, posterior surfaces of the laminae on anterior thoracic ribs are similarly flat, but become progressively modified into a deep concavity by the anteroposterior lengthening of the capituli and tuberculi and by the posterior migration of the former (*cp*, Fig. 12B). Facing pairs of concavities, one anterodorsal, another posteroventral, thus form a wide sinus adjacent to each intervertebral foramen in the posterior thoracic and lumbar series.

The most bizarre feature of the presacral ribs in *Thrinaxodon* and in many other cynodonts is the localized expansion of each shaft, conveniently referred to as a costal plate (*p*, Fig. 12). No single description of a cynodont costal plate would suffice because costal plates are structurally very different not only with respect to vertebral regions, but also among cynodont families. A description of the costal plates in *Thrinaxodon* may conveniently begin with those on the anterior thoracic ribs; the cervical costal plates were probably similar to the anterior thoracics, but, as indicated in the preceding section, are known only from poorly preserved material. The dorsal edge of the tubercular process is thin and blade-like in the anterior thoracic ribs and is confluent laterally with the rising dorsal margin of the costal plate (Fig. 12A). At the fourth or fifth thoracic rib, however, the costal plates of the ribs become differentiated from the dorsal edge of the capitular process by an incipient costal tubercle (*tbc*, Fig. 12A, C) which becomes progressively larger in the remaining thoracic and lumbar series. Typically developed from the sixth thoracic rib posteriorly, the costal tubercle is a bulbous swelling on the dorsomedial edge of the costal plate. Between the costal tubercle and the transverse process the dorsal edge of all thoracic capitular processes posterior to the sixth thoracic rib becomes anteroposteriorly broader as well as transversely wider. Beginning with the fifth or sixth thoracic rib each of these broad dorsal edges is grooved anteroposteriorly (*gr*, Fig. 12A), creating the impression of a paraxial sulcus which extends to the sacrum but which is partitioned transversely by the intercostal spaces.

The costal plates of the thoracic ribs display a complex morphological gradient which is partly obscured by their imbricating relationship. In all thoracic ribs except the 13th the shaft is continuous between the capitulum and the distal costal shaft by means of a distinct ridge across the ventral side of the costal plate (*cap*, *sh*, Fig. 12B). On the 13th thoracic and first lumbar this ridge is discontinuous and on all the following lumbar ribs it is lost. The costal plate of an anterior thoracic rib is basically a vertical, supracostal flange arising from the dorsal aspect of the rib shaft; only a small part of the plate extends ventrally below the rib shaft. The external surface of an anterior thoracic plate faces anterolaterally and is shallowly concave by virtue of the lateral reflection of the incipient costal tubercle above and the ventral edge of the plate below.

The costal plates of the middle and posterior thoracic ribs progressively undergo the following changes. The costal tubercle differentiates as a bulbous, ventral reflection of the otherwise nearly horizontal costal plate; the remainder of costal plate faces dorsally and slightly anterolaterally. The posterior half of the costal plate expands and lies on the anterior half of the next posterior plate, resulting in extensive imbrication of adjacent plates. The posterior edges of the fifth through tenth thoracic costal are swollen and in effect form a second costal tubercle, a feature absent on all remaining thoracic and lumbar ribs.

The costal tubercles of thoracic ribs are aligned parasagittally with those of the lumbar ribs which in turn are aligned with the iliac blade (Fig. 12A). Thus the axial skeleton shows a major subdivision along the line of the costal tubercles: the costal plates and shafts lie laterally, and a broad channel lies medially between the tubercles, or iliac blade, and the neural spines. The width of the channel, measured from the apex of the costal tubercle to the sagittal plane, is greatest at the level of the twelfth and thirteenth thoracic vertebrae (13.1 mm in AMMM 5265) and is only slightly less at the fifth thoracic (11.4 mm) and at the seventh lumbar (11.9 mm). Anterior to the fifth thoracic rib the channel is difficult to define because of the rib reorientation and diminution of the costal tubercles.

The largest costal plates in terms of area are estimated to be those of the eleventh to thirteenth thoracic ribs. Accurate measurement of the relative sizes of costal plates requires a disarticulated skeleton.

Little can be described of the rib shafts which extend beyond the costal plates because they are very slender and commonly are either lost or damaged. In anterior thoracic ribs the shaft comprises about three-quarters of the rib length. On the seventh and eighth thoracic ribs the shaft is estimated to have been a little over half the rib length. On the 10th thoracic the shaft is considerably shortened and on the 13th it is a mere spike. Each of the first three lumbar ribs bears a tubercle; the tubercles successively decrease in size from first to third. No vestige of a rib shaft can be detected on the fourth through seventh lumbar ribs.

Thoracic rib shafts preserved with USNM 22812 are extremely compressed in cross-section. The posterior aspect of the shaft, as it emerges from under the costal plate, bears a deep, longitudinal groove. As the groove runs along the shaft, it comes to lie more on the dorsal aspect of the shaft. The groove, which cannot be traced to its terminus because no thoracic rib is sufficiently complete, probably represents an intercostal neurovascular sulcus.

Lumbar Ribs

MORPHOLOGY. Lumbar ribs are synostosed to the transverse processes along a serrate suture and the articulation is not "loose" as suggested by Brink (1958: 21). The capitular processes become progressively shorter toward the sacrum and shift dorsally to closer proximity with the tuberculi. Therefore lumbar capitular processes reverse the trend of the thoracic series in which the capituli become progressively longer and move lower on the centrum rim. Lumbar capitular articulations also shift posteriorly until, at the sixth lumbar, the capitulum contacts only the centrum of the sixth lumbar and the articulation is no longer intervertebral. The tuberculi of all lumbar ribs are broad. With the possible exception of the first two or three lumbar ribs, it appears that lumbar capitular and tubercular facets are essentially confluent and thus fuse with a synapophysis.

The costal plates of the lumbar ribs are gradually transformed from the lanceolate shape of the thoracic plates to a subrectangular outline (Fig. 12C). In the lumbars the costal tubercle becomes anteroposteriorly longer and narrower (Fig. 12A). The plates continue to imbricate so that the long, narrow costal tuberosities form an undulating ridge of bone which is aligned parasagittally with the iliac blade. The ventral parts of the costal plates are reduced in size relative to the analogous area on thoracic costal plates; furthermore, they are gradually reoriented to face more laterally and less dorsally.

The anterior margins of lumbar costal plates are concave and do not extend significantly forward of the conjoined capitular and tubercular processes. Such a construction permits the convex medial surface of one costal plate to project posteriorly over the concave lateral surface of the next (posterior) costal plate (Fig. 12C).

As a series the lumbar plates become progressively smaller toward the ilium. The height of the seventh lumbar costal plate equals that of the adjoining ilium and the dorsal and ventral edges of the costal plate and iliac blade are continuous. In AMMM 5265, Fig. 12C, both ilia have been displaced dorsally post-mortem. Furthermore the posterior margin of the seventh lumbar costal plate contacts the anterior margin of the iliac blade, making the lateral surfaces of the ilium and lumbar plates continuous.

SACRAL RIBS

MORPHOLOGY. All five sacral ribs are fused to synapophyses. Not only are the capitular and tubercular facets confluent, as they are on lumbar ribs, but the capitular and tubercular processes also fuse and cannot be distinguished. In the lumbar ribs the processes are closely conjoined but can be morphologically delineated. The first sacral rib is the largest. Its costal plate, which is as long but not as high as that of the seventh lumbar, bifurcates anteriorly. The dorsal and ventral parts of this bifurcation clasp the medial side of the seventh lumbar costal plate. The ventral part, which is the larger of the two parts, extends anteriorly to overlap on the lower medial surface of the seventh lumbar costal plate (*S1*, Fig. 12B); the smaller dorsal part similarly overlaps the upper medial surface (*S1*, Fig. 12A, left side). The remainder of the first sacral rib plate, posterior to the bifurcation, contacts the medial surface of the ilium, thus forming a bond between the seventh lumbar costal plate and the pelvis. The second through the fourth sacral ribs progressively diminish in size and do not bear costal plates, although the second and third sacral ribs are slightly expanded at their iliac contact. All sacral ribs are directed laterally and, with the exception of the fifth sacral, their distal ends are flattened dorsoventrally and elongated anteroposteriorly. The fifth sacral rib is approximately triangular in shape (Fig. 12A, left side). The apex of the triangle contacts the transverse process. The anterior corner of the triangle is a slender rod which passes anterolaterally to contact the posterior, medial extremity of the ilium (see AMNH 2228). The posterior corner of the triangular rib passes posterolaterally to make contact with the first caudal rib. The nature of this contact is not sufficiently preserved in any specimen to permit description.

The sacroiliac joint is not synostosed and probably represents a synchondrosis. In most specimens (including AMMM 5265) the ilia are either displaced or are altogether disarticulated from the sacral ribs.

Caudal Ribs

MORPHOLOGY. Ribs are preserved with the first four caudal vertebrae of AMNH 2228. The capitulum and tuberculum are fused and cannot be distinguished. Each shaft is swollen at the contact with the transverse process, is constricted about the middle, and expands anteroposteriorly at the lateral terminus. The lateral terminus is dorsoventrally flattened. It is probable that the first and second and second and third ribs made contact by virtue of their lateral expansion, but the nature of this contact is not clear. The fourth caudal rib is dumbbell-shaped and much smaller than the others. All caudal ribs are directed posterolaterally and somewhat ventrally.

4. THE POSTCRANIAL AXIAL SKELETON OF OTHER GALESAURIDS

MATERIAL. Parrington (1934) described the vertebral column and rib morphology of *Galesaurus* from three specimens collected in the *Lystrosaurus* zone near Harrismith. Two of the specimens, one an isolated and incomplete lumbosacral series with the third lumbar through second sacral vertebrae (UMC R.2733), the other an almost complete vertebral column with the second through fourth sacral vertebrae (UMC R.2722), are not associated with any diagnostic cranial remains. Generic identification was founded primarily on the presence of anapophyses (Parrington, pers. comm.) which are also present in the third specimen consisting of a *Galesaurus* skull and the first four cervical vertebrae (UMC R.2721). Anapophyses are common to the vertebrae of most cynodonts, however, and the generic assignment of the first two specimens is in doubt. Nevertheless the vertebrae are unquestionably galesaurid and are, in fact, indistinguishable from *Thrinaxodon* itself. Since this generically unidentifiable material reveals certain features not clearly seen in other galesaurid specimens, it will be accorded further description. In addition the cervical vertebrae of Parrington's third specimen, which is assuredly *Galesaurus*, and six thoracic vertebrae and ribs of another positively identified *Galesaurus* (SAM K.1119) will be described. They, too, are indistinguishable from *Thrinaxodon* material and provide a clearer understanding of the galesaurid axial morphology.

Cervical Series

MORPHOLOGY. The third through seventh cervical vertebrae are indistinguishable from those of *Thrinaxodon*. The neural spines of the third, fourth and fifth cervicals are fusiform in cross-section, taper towards the apex, and are recurved posteriorly. The spine of the third cervical is the most sharply recurved to permit space for the posteriorly projecting axis blade. The anteroposterior ridge across the dorsal laminar surface appears to be relatively higher, although in this specimen the lateral edges of the zygapophyses are missing. The angles of zygapophyseal articulations and the morphology and orientation of the robust transverse processes are the same as in *Thrinaxodon*. Parrington (1934: 49) claimed that the zygapophyseal articulation between the third and fourth cervical is "rather more horizontal" than that between the axis and the third cervical. In fact the reverse is true; as in *Thrinaxodon*, the articulation of the zygapophyseal facets of the axis and third cervical makes an angle of approximately 45° with the horizontal and between the third and seventh cervical vertebrae the angle increases to about 55°. On UMC R.2722 the articulations show the same features, although they are somewhat obscured by breakage.

Thoracic Series

MORPHOLOGY. In the 13 thoracic vertebrae of UMC R.2722 no substantial differences from *Thrinaxodon* are apparent although the specimen is only partially prepared and somewhat damaged. The morphological gradient of facets for the tuberculum is evident. In the anterior thoracic vertebrae the capitular fovea is composed of two separate demifacets borne on the adjacent rims of successive vertebrae. These demifacets, located on the dorsolateral aspect of the rim below the pedicle-centrum suture, together form a wedge-shaped fovea. The caudal demifacet is partially formed on the base of the pedicle projecting anteriorly beyond the rim of the centrum. Toward the posterior thoracic vertebrae, the fovea progressively increases in size and shifts its position caudally, i.e., by increasing the demifacet size of the caudal half and decreasing the demifacet size of the cranial half.

In the most anterior thoracics the transverse process is crescentic in cross-section (*tr p*, Fig. 13A). An anteroventral extension of the process almost reaches the pedicle-

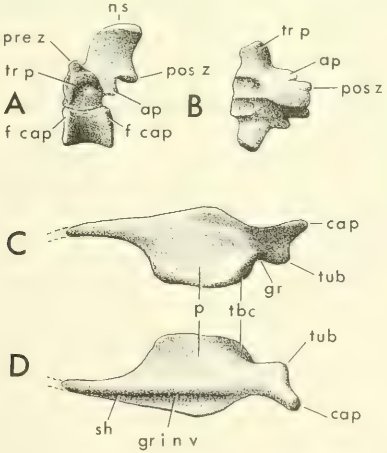

FIG. 13. *Galesaurus planiceps,* SAM K. 1119. A, lateral; B, dorsal views of first or possibly second thoracic vertebra. C, dorsal; D, ventral views of fifth or possibly sixth thoracic rib. Approx. X1.5. Abbreviations as in FIG. 12 except: *gr i n v*, groove for intercostal nerve and vessels; *n s*, neural spine; *pos z*, postzygapophysis; *pre z*, prezygapophysis.

centrum suture, while a posteroventral extension reaches the base of the anapophysis. For the most part the facet for the tuberculum faces laterally. In the more posterior thoracics the facet becomes less crescentic and more fusiform in cross-section as the size of the cranial capitular demifacet increases and as the facets for the capitulum and tuberculum nearly merge. In the lumbar vertebrae both facets are confluent.

An acid-prepared specimen of *Galesaurus* (SAM K.1119) preserves a series of six thoracic vertebrae which are completely freed of matrix and on which further and more detailed observations can be made than is possible on the Cambridge specimens. The vertebrae are distinguished from the cervical series by their relatively low, anteroposteriorly wide neural spines, and from the lumbar series by the character of their associated ribs (see below, p. 66). The vertebrae, which are hereafter referred to numerically, 1—6, are tentatively identified as being the first through the sixth thoracic vertebrae, or possibly the second through seventh. This identification is made possible by certain morphological changes which are comparable to those in the anterior thoracics of *Thrinaxodon* (AMMM 5265) and *Galesaurus* (UMC R.2722). The height of the neural spines, measured from the apices to a horizontal line tangential to the dorsal rim of the prezygapophyses, decreases from 7 mm at 1 to 4 mm at 6. Neural spines of posterior thoracic vertebrae in *Thrinaxodon* do not show this degree of differentiation (see p. 54). The six vertebrae also show an increase in the transverse breadth of the neural spine base, as in the anterior thoracics of *Thrinaxodon* (AMMM 5265).

The demifacets for the capitulum are poorly preserved in SAM K.1119 and are restored in the vertebra illustrated (*f cap*, Fig. 13A). The loss of this feature is partly the result of acid preparation which separated the vertebra along the pedicle-centrum suture; this region was apparently incompletely ossified. The morphology of the transverse process and its facet for the tuberculum is clearly shown, however, and is identical to those on the anterior thoracic vertebrae of UMC R.2722.

The zygapophyses are well preserved and permit detailed description of features obscured in other articulated specimens. The articular facets of the prezygapophyses are rounded, cuplike depressions which are open dorsally and anteriorly (Fig. 13B). If flattened out, the facet would be oval in outline with the long axis transverse to the vertebral axis. The prezygapophyses are not the typical protruding processes or "stalks", for part of the articular facets are actually recessed within the laminae. Each facet is composed basically of a nearly vertical wall laterally and a nearly horizontal floor medially. The two horizontal sectors are separated medially by a ridge which is an anterior continuation of the neural spine.

The postzygapophyses are distinct processes protruding posteriorly from the base of the neural spine (*pos z*, Fig. 13A, B) and are separated by a groove which receives the basal part of the spine of the succeeding vertebra. They extend beyond the rim of the centrum in order to couple with the prezygapophyses recessed in the laminae of the succeeding vertebra. A posterior articular facet is divisible into lateral and ventral surfaces, corresponding in orientation to the lateral wall and medial floor of the prezygapophyses. In previous discussion of the angle of interzygapophyseal articulation in *Thrinaxodon*, only the orientation of the lateral aspect of the facet could be estimated because the medial (horizontal) part of the facet was obscured by the articulation. The six vertebrae of *Galesaurus* show that the orientation of the lateral (vertical) aspect of the zygapophyseal facets is progressively modified in the anterior thoracic series, as in *Thrinaxodon*, although the medial (horizontal) aspect, obscured in the AMMM 5265 *Thrinaxodon*, persists unchanged. The exact degree of facet reorientation is difficult to determine because the delicate facets have been somewhat deformed plastically. The orientation of facets relative to the sagittal plane was estimated by protractor from photographs taken of each vertebra in anteroposterior view. The lateral aspect of the prezygapophysis of the first vertebra is estimated to be 10° (±5°) to the sagittal plane, while that of the postzygapophysis of the same vertebra is 14° (±5°). Using the same technique the lateral prezygapophyseal aspect of the sixth vertebra is approximately 25° (±5°) and that of the postzygapophysis is 33° (±5°). Despite the uncertainties engendered by plastic deformation, the zygapophyseal reorientation toward a more horizontal plane is definitely demonstrated.

An increase in the length of the laminae, measured anteroposteriorly between the tips of the zygapophyses, characterizes these vertebrae as it does the thoracics of *Thrinaxodon*. On the first vertebra the length is 9 mm and it increases at each successive vertebra to 10.2 mm on the sixth.

As in the anterior thoracics of *Thrinaxodon* the transverse processes of the six vertebrae are directed laterally and slightly anteriorly and progressively increase in anteroposterior breadth, viewed from above. The degree of cranial inclination is greater at the first vertebra than at the sixth. These vertebrae also show the same progressive modification of the tubercular facet seen in *Galesaurus* (UMC R.2722) and *Thrinaxodon*. The incipient anteroventral extension of the transverse process on the first vertebra (*tr p*, Fig. 13A) increases in thickness and extent so that at the sixth vertebra the facets for the capitulum and tuberculum are nearly confluent.

Lumbar Series

MORPHOLOGY. The lumbar series of UMC R.2722 is probably composed of seven vertebrae as in *Thrinaxodon*, but it is impossible to verify the count because the lumbar ribs are poorly preserved and the lumbosacral articulation is not exposed. Parrington (1934: 51) believed the 28th vertebra to be a lumbar, which would give a total count of eight lumbar vertebrae, assuming that there were 13 thoracics as in *Thrinaxodon*. However, the prezygapophyseal articulation of the 28th vertebra is sufficiently preserved on the left side to show that the interzygapophyseal breadth is reduced relative to that of the 27th vertebra, i.e., the seventh lumbar vertebra. This same feature is characteristic of the interzygapophyseal articulation between the seventh lumbar and first sacral in *Thrinaxodon* and on this basis the 28th vertebra would appear to be the first sacral—not a lumbar as suggested by Parrington. The cranial edge of the iliac blade is broken off in this specimen but if reconstructed would overlap the transverse process of the vertebra in question and thus substantiate its sacral position. Therefore the presacral vertebral count in *Galesaurus* is probably the same as in *Thrinaxodon*, i.e., seven cervicals, thirteen thoracics, and seven lumbars; furthermore, the morphology of the vertebrae cannot be shown to be recognizably different on the basis of UMC R.2722 and SAM K.1119.

SACRAL SERIES

MORPHOLOGY. The sacrum of UMC R.2722 is so poorly preserved and incompletely prepared that little can be added to Parrington's description. As in the sacrum of *Thrinaxodon* the neural spines are more slender than those of the lumbar series and the zygapophyseal articulations are nearly vertical. The iliac blade extends sufficiently posteriorly to have included a fifth sacral vertebra which would be numbered 32 in the complete vertebral column. Unfortunately the posterior half as well as the transverse processes of this vertebra have been broken away, but the mere length of the iliac blade is evidence that the sacrum includes five vertebrae as in *Thrinaxodon*.

RIBS

MORPHOLOGY. The only ribs positively associated with *Galesaurus* (SAM K.1119) are from the thoraic region. These ribs are best preserved on the left side and belong to the middle four of six vertebrae, which are all that remain of the vertebral column. The vertebrae with which they are associated are either the second through fifth or third through sixth thoraic (see above, p. 64). In no way can these ribs be shown to differ from comparable anterior thoracic ribs of *Thrinaxodon*. However, since these ribs display several features more clearly than in any specimen of *Thrinaxodon*, and because they have been acid-prepared and disarticulated, further description of these aspects is warranted.

The articular facets of the capitulum and tuberculum are well preserved on the fourth rib, i.e., the fifth or sixth thoracic (Fig. 13C, D). The capitular facet is small, circular and slightly convex; it obliquely truncates the terminus of the capitular process. The tubercular facet is straight and narrow, extending from the tubercular process along the capitular process almost to the capitular facet. It is slightly narrower than the capitular facet. The dorsal third of the facet faces medially, the central third posteromedially and the ventral third medially again. The ventral third sharply attenuates and does not reach the end of the capitular process. The dorsal half of the facet is flat but the ventral half is slightly concave. The orientation and the surface relief of both facets probably vary with ossification or position and these features should not be regarded as constant. For example, the 11th (or possibly the 12th) thoracic rib associated with ?*Galesaurus* (UMC R.2722) has a capitular facet which is round and bulbous and a tubercular facet which is concave along its entire length and faces medially with no posterior twisting of the center section.

In *Thrinaxodon* the thoracic ribs posterior to the fifth, as well as all lumbar and sacral ribs, show a distinct anteroposterior groove across the dorsal edge of the tubercular process (*gr*, Fig. 12A; see p. 59). This groove is incipiently developed in the anterior thoracic ribs, but becomes progressively wider and longer with the successive increase in size of the thoracic and lumbar tubercular processes. The preservation of the first four thoracic ribs in *Thrinaxodon* (AMMM 5265) does not reveal the details of this region. On *Galesaurus* (SAM K.1119), however, the morphology is clear. On the rib of vertebra five, i.e., either the fifth or sixth thoracic, the edge is rather narrow but the groove is incipiently developed (*gr*, Fig. 13C). The analogous area on ribs of vertebrae two, three and four is exceedingly blade-like and straight and all traces of the groove between the tuberculum and costal tubercle are lost.

The imbrication of the costal plates in *Thrinaxodon* (AMMM 5265) obscures certain details that are evident in the disarticulated ribs of *Galesaurus* (SAM K.1119). The anterior margin of the plate is slightly convex and reflected dorsally (Fig. 13C). As the posterior margin is also reflected dorsally especially near the costal tubercle, the entire dorsal surface is gently concave. A shallow groove adjacent and parallel to the anterior margin receives the posterior ventral surface of the preceding costal plate. A deep groove, perhaps representing the course of an intercostal nerve and vessels, typically occurs on the ventral surface of a plate between its anterior lip and the shaft (*gr i n v*, Fig. 13D). This groove continues distally on the shaft beyond the terminus of the costal plate, and gradually fades out 1 cm from the costal plate. As it fades out it shifts its position toward the dorsal aspect of the shaft.

5. THE POSTCRANIAL AXIAL SKELETON OF *CYNOGNATHUS*

MATERIAL. *Cynognathus crateronotus* was described and figured by Seeley (1895b) from an incomplete and crudely prepared skeleton of a single individual (BMNH R.2571). The axial skeleton is relatively complete, although the posterior caudal vertebrae are missing as are most of the cervical and thoracic ribs. There has never been any further detailed investigation into the axial morphology of this well-known cynodont genus, primarily for lack of new material. In addition to the type material very fragmentary remains are known from two collections (BPI 1675; NMB C.2710 and NMB C.2713) in which disarticulated remains of many individuals of this genus and *Diademodon* are preserved together. In addition there is an incomplete and somewhat crushed skeleton of a single individual of *Cynognathus* sp. (UCMP 42729). Broili and Schröder (1936) have described the axis and several cervical vertebrae from a large cynodont believed to be *Cynognathus*. All of the above material, even if considered together, does not permit a complete evaluation of the *Cynognathus* axial skeleton. Nevertheless certain differences as well as similarities to other cynodonts are worth describing.

CERVICAL SERIES

MORPHOLOGY. The atlas-axis complex, insofar as known, is basically similar to that in other cynodonts. The primary differences are the rather rectangular outline of the first intercentrum and the more ventral orientation of the intercentral facet on the atlas centrum.

The number of cervical vertebrae in *C. crateronotus* (BMNH R.2571) is seven, not six as suggested by Seeley (1895b: 97). The division between cervical and thoracic vertebrae is based on the same criteria as in *Thrinaxodon*. First, the prezygapophyses of the seventh cervical and the zygapophyses of all vertebrae anterior to this vertebra are inclined at an angle of about 45°. The postzygapophyses of the seventh cervical and the zygapophyses of the anterior thoracic vertebrae are nearly vertically inclined. Second, the transverse processes of the first six cervical vertebrae are directed posterolaterally and ventrally; the transverse processes of the seventh are approximately at the same level as are those anterior to it, contrary to Seeley's claim, but they are directed laterally only. The transverse process of thoracic vertebrae are directed more or less anterolaterally as in *Thrinaxodon*.

The cervical vertebrae of *Cynognathus crateronotus* (BMNH R.2571) are similar to those of *Thrinaxodon* in a number of features. The neural spines are fusiform in cross-section and are slightly recurved caudally. The spine of the seventh cervical vertebra, although broken off near the base, appears to have been intermediate in cross-section between the slender cervical spines and the wider, more robust thoracic spines. The width between zygapophyses is greatest at the cranial end of the cervical series and continues to diminish throughout the anterior thoracic series as in *Thrinaxodon*. Intercentra are associated with the first six vertebrae and possibly with the seventh as well; the interspace of the sixth and seventh cervical vertebrae is obscured by a displaced rib. As in *Thrinaxodon* the ventral aspect of the cervical centra bears a longitudinal keel along the midline. The keel is most prominent on the axis and diminishes in size on succeeding centra until on the first and second thoracic vertebrae it is merely a swelling. Anapophyses are absent in *Cynognathus* cervical vertebrae (see Broili and Schröder, 1936: 66).

THORACIC SERIES

MORPHOLOGY. There are 15 thoracic vertebrae in *Cynognathus crateronotus* (BMNH R.2571), two more than in *Thrinaxodon*. The first lumbar is distinguished from the 15th and last thoracic by the character of its associated rib (discussed below); otherwise, there is no sharp morphological discontinuity between thoracic and lumbar vertebrae. Insofar as may be determined from the partially prepared type material, the thoracic vertebrae are morphologically similar to those of *Thrinaxodon*. A gradual and very slight increase in the length of centra is evident. The total increase is approximately ~~3 mm~~ from the anterior thoracics, which measure 29 mm, to the posterior thoracics, which measure about 32 mm.

The zygapophyseal facets of the anterior thoracics are inclined nearly vertically. This condition prevails throughout most of the thoracic series, but in the 13th through 15th thoracics, and in the lumbar series as well, there appears to be a shift towards a more horizontal orientation. The incompleteness of preparation, however, does not permit verification of this reorientation, which is positively known in *Thrinaxodon*.

The neural spines of the thoracic vertebrae are shorter than those of the cervicals; they differ from the thoracic spines of *Thrinaxodon* in being less triangular and more fusiform in cross-section.

Another difference is in contour of the dorsal surface of the transverse processes. In *Thrinaxodon* the dorsal surface of all thoracic transverse processes are essentially cylindric, being smoothly convex from front to back. In *Cynognathus* the dorsal surface of the first through tenth thoracic transverse processes are convex anteriorly, similar to those in *Thrinaxodon*, but posteriorly there is a transverse groove not represented in *Thrinaxodon*. The remaining transverse processes are as in *Thrinaxodon*.

Lumbar Series

MORPHOLOGY. There are seven lumbar vertebrae as in *Thrinaxodon*. The length of each lumbar centrum in BMNH R.2751 is the same as that of a posterior thoracic centrum. There is a gradual and slight increase in the width of lumbar centra from 25 mm at the second lumbar to 28 mm at the seventh. The transverse width between prezygapophyses continues to increase, as in the thoracic series; on the first lumbar the width is 23 mm, while on the seventh it is 25 mm. Conversely the transverse width between the tubercular facets on the transverse processes decreases. The maximum width is reached and maintained at about 56 mm from the posterior cervicals through the 14th thoracic vertebra; on the 15th thoracic the width decreases to about 53 mm and on subsequent vertebrae continues to decrease until at the seventh lumbar it measures 44 mm. In these and other proportions the lumbar vertebrae of *Cynognathus* resemble those of *Thrinaxodon*. Only in the narrow, somewhat more fusiform shape of the lumbar neural spines of *Cynognathus* is there any significant difference from *Thrinaxodon*.

Sacral Series

MORPHOLOGY. Only three sacral vertebrae are preserved with the type of *C. crateronotus* (BMNH R.2571); however, the length of the associated iliac blade makes it probable that there were five sacrals as in *Thrinaxodon*. Their preservation and preparation is so poor that only a superficial comparison may be made with the sacrals of *Thrinaxodon*. As in the latter, the sacral centra are about the same length as those of the lumbar region, but tend to be narrower and more constricted about the middle. The transverse distance between prezygapophyses is much reduced, approximately 15 mm compared with 25 mm at the seventh lumbar, and the zygapophyseal facets are inclined nearly vertically. The transverse distance between the distal ends of the transverse processes is only slightly reduced, 41 mm, or 3 mm less than at the seventh lumbar. In cross-section the transverse processes are much less robust than in the lumbar series. Measured at the base, the heights of the seventh lumbar and first sacral transverse processes are 33 mm and 26 mm, respectively; the respective anteroposterior lengths are 19 mm and 14 mm. The second and third sacral vertebrae are even smaller in these dimensions. All of these features are comparable to those developed in *Thrinaxodon* sacrals. No significant differences were detected.

CAUDAL SERIES

MORPHOLOGY. Associated with the type of *C. crateronotus* are four and one-half vertebrae which probably are part of the caudal series. The centra are markedly shorter and narrower than those of the sacrum and it therefore seems unlikely that these represent the most anterior caudal vertebrae. Like the caudal vertebrae of *Thrinaxodon* the zygapophyseal articulations are oriented within 10°–20° of the sagittal plane. The transverse processes are all lost.

The exact number of caudal vertebrae in larger cynodonts such as *Cynognathus* is unknown. A specimen (NMB R.531) tentatively referred to *Diademodon* by Brink (1955) possesses at least eight caudal vertebrae. However this specimen lacks the skull and therefore cannot be positively distinguished from *Cynognathus*. It clearly demonstrates that marked diminution of caudal vertebra size occurs among the first four vertebrae and thus this cynodont's tail was relatively short.

CERVICAL RIBS

MORPHOLOGY. The only known cynognathid cervical ribs are preserved with *C. crateronotus* (BMNH R.2571). These include an incomplete axis rib and ribs of the sixth and seventh cervical vertebrae.

The proximal end of the axis rib is expanded into a flat, triangular plate. Dorsally one corner is the tuberculum, which articulates with the axis transverse process. The apex of the triangle is represented by the capitulum, which has been displaced anterodorsally post-mortem. During life the capitulum probably articulated between the axis and atlas centra, as in other cynodonts, and not on the atlas centrum, where there is no facet as claimed by Seeley (1895b: 102). The third corner is a flat, blunt process projecting ventrally from the plate. From the base of the triangular plate arose the distal shaft of the rib, which is broken off in this specimen. A sharp crest crosses the external surface of the plate from the base of the shaft to the base of the capitular process. The crest appears to have been continued distally along the shaft but proximally it does not reach the end of the capitulum.

The sixth and seventh cervical ribs are substantially different from the axis rib. The proximal ends of these ribs lack the development of a triangular plate. On the sixth cervical rib the wide capitulum and tuberculum bifurcate from the shaft at approximately the same level, forming a Y-shaped structure; on the seventh the capitulum is a straight continuation of the shaft, the tuberculum diverging at an angle of almost 80°. Although poorly preserved, both capituli and tuberculi appear to be thicker and more robust than their counterparts on the axis rib. A sharp median ridge from the ventrolateral aspect of both shafts continues to the proximal end of each rib between the capitulum and tuberculum. It is apparently homologous with the similar ridge on the axis rib shaft and plate. The only tendency toward a costal plate is the slight swelling of the dorsal margin of the rib adjacent to the tuberculum. This condition is suggestive of the cervical ribs of *Thrinaxodon* in which an extensive, hemicircular flange arises from the dorsal margin of the shaft adjacent to the tuberculum.

Thoracic Ribs

MORPHOLOGY. In the type of *C. crateronotus* (BMNH R.2571) the first through 11th thoracic ribs are either completely lost or are broken off immediately distal to the capitulum and tuberculum. However the general structure of the anterior thoracic ribs may be inferred from a number of isolated specimens (BPI 1675; NMB C.2710; UCMP 42729). The morphological gradients that characterize these ribs cannot be described at present. The type of *C. crateronotus* shows that the 12th through 15th thoracic ribs as well as those of the lumbar series bear costal plates.

In *Cynognathus* the anterior thoracic ribs do not bear costal plates. The rib or ribs at which the costal plate is first differentiated and subsequently comes to overlap the succeeding ribs are not known. Some isolated ribs (UCMP 42729), interpreted as belonging to the most anterior thoracics, are devoid of any structure suggestive of an incipient costal plate (Fig. 14A). In these the long capitular process is straight, makes an angle with the neck of about 45°, and widely separates the capitular facet from the tubercular facet. The proximal end of the capitular process is expanded to bear an oval or round facet. The tubercular facet is an elongate oval, the long axis of which is oriented dorsoventrally. The proximal shaft is crescentic in cross-section, being somewhat convex anteriorly and concave posteriorly. Other ribs associated with the same specimen (UCMP 42729), interpreted as belonging to the middle of the thoracic series, possess a shorter, less expanded capitular process and a distinct ridge along the center of the anterior aspect of the shaft (*r c p*, Fig. 14B, C). This ridge, together with a posterior reflection of the shaft's dorsal edge adjacent to the tubercular process, apparently represents the initial differentiation of the costal plate.

Of the posterior thoracic ribs, only the 12th through the 15th are known in *C. crateronotus*. These ribs bear well-developed costal plates that are quite different from those of *Thrinaxodon*. In size the costal plates are relatively smaller than in *Thrinaxodon* and are basically diamond-shaped (*p*, Fig. 15A). The plate may be visualized as consisting of anterior and posterior flanges separated ventrally by a ridge which represents the original rib shaft. As in *Thrinaxodon* the anterior flange is the smaller of the two. Its margin is symmetrical and thicker medially than laterally. In general the thickness of the flange decreases anteriorly, i.e., toward the anterior margin. The posterior flange is asymmetrical and separated from the shaft by a very shallow groove on the dorsal and ventral surfaces. Thus this flange is rather thin along its junction with the rib shaft and is thicker along its posteromedial margin. Like the anterior flange margin, the margin of the posterior flange is blade-like and somewhat rugose.

The orientation of the proximal part of the 12th thoracic rib, and probably those of the 9th, 10th and 11th thoracic ribs as well, is approximately transverse to the sagittal axis. The capitular process lies almost directly ventral to the tuberculum and the neck of the rib passes laterally to the costal plate. The distal shaft of the rib, emerging from the ventral surface of the plate, then passes posteroventrally. The 13th, 14th and

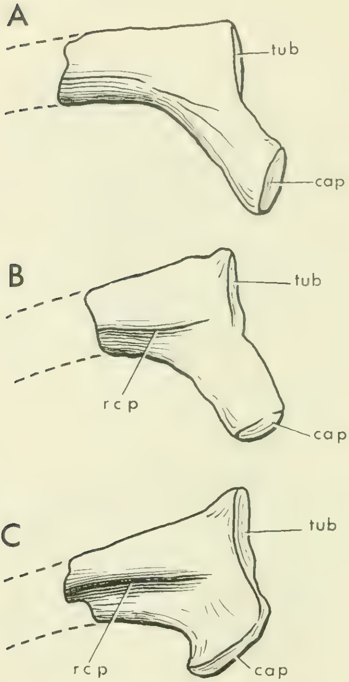

FIG. 14. Proximal ends of anterior and middle thoracic ribs of *Cynognathus* sp., UCMP 42729, in anterior view. A, B and C are interpreted as representing ribs successively more posterior in position in the thoracic series. X1. Abbreviations as in FIG. 12 except: *r c p*, ridge on anterior aspect of rib shaft representing incipiently developed costal plate.

15th thoracic ribs, however, undergo a reorientation of the neck that is carried over into the lumbar series. The neck in these ribs is directed more anterolaterally, instead of laterally (Fig. 15A). At the same time the neck is progressively modified from an anteroposteriorly narrow shaft to a broad shaft, while retaining approximately the same depth as in the 12th thoracic rib.

The costal plates of the 12th and 13th thoracic ribs develop a ridge along the posteromedial border of the dorsal surface (*r*, Fig. 15A). This ridge arises at the junction of the costal plate and the proximal part of the rib shaft and runs obliquely to the shaft axis, ending at the lateral margin of the posterior flange. On the 14th thoracic rib the position and proportions of this ridge resemble those of the costal tubercle developed in *Thrinaxodon*. On the 15th thoracic rib the ridge, here much enlarged,

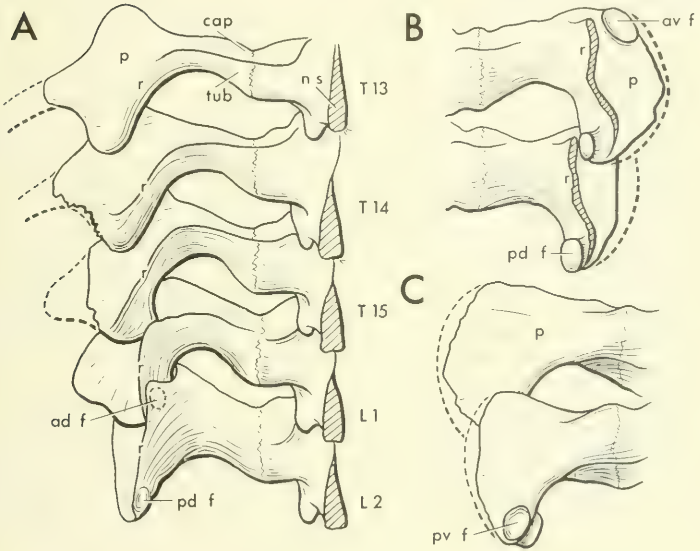

FIG. 15. Lumbar ribs of the *Cynognathus—Diademodon* pattern. A, dorsal view of thirteenth thoracic through second lumbar vertebra of *Cynognathus crateronotus*, BMNH R.2571. B, dorsal; C, ventral views of unassociated lumbar rib plates of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, showing placement of facets. Approx. X0.5. Abbreviations as in FIG. 12 except: *ad f*, anterodorsal facet; *av f*, anteroventral facet; *pd f*, posterodorsal facet; *pv f*, posteroventral facet; *r*, ridge on costal plate. For details, see text.

extends almost to the anterior edge of the plate and is more oblique to the axis of the rib shaft. On the following rib, the first lumbar, the crest of the ridge is reflected laterally to such an extent that the posterior flange of the 15th thoracic costal plate is gripped in pincer-like fashion between the ridge and the dorsal surface of the first lumbar costal plate. This arrangement is further elaborated in the lumbar region described below. It may be noted here, however, that disarticulated rib plates (especially UCMP 42729) possess slightly raised, oval articular facets at the points of plate overlap; this feature, too, is repeated in the lumbar series.

In the type of *Cynognathus* the 14th and 15th thoracic ribs are synostosed to their transverse processes along distinct, serrate sutures. The 12th and 13th thoracic ribs are probably synostosed. The shafts of the 10th and 11th thoracic ribs are broken across the neck, although the capituli and tuberculi still are articulated, and it appears possible that these ribs were also synostosed. The presence of adherent matrix on the type, especially at the rib articulation of the 10th and 11th thoracic ribs, makes the nature of the articulation difficult to interpret. However the transition from unfused ribs in the middle thoracic series to fused ribs in the posterior thoracic series is analogous to the condition in *Thrinaxodon.*

LUMBAR RIBS

MORPHOLOGY. The lumbar region is distinguished from the thoracic on the basis of rib morphology. The first lumbar vertebra is here defined as the first dorsal vertebra bearing a costal plate that grips the preceding costal plate, i.e., the 15th thoracic, by a lateral reflection of its dorsal ridge (*r*, Fig. 15A). In addition, all lumbar ribs lack shafts or shaft vestiges distal to the costal plate. However, the morphological transition between thoracic and lumbar ribs is gradational. The decision as to which costal plate first achieves the interlocking mechanism and loses the distal rib shaft is somewhat arbitrary as Figure 15A shows; during lateral flexure the 15th thoracic rib obviously might interlock with the 14th thoracic rib. Nevertheless the lumbar and thoracic series are quite distinct with respect to rib morphology, despite their intergradation, and deserve separate recognition.

The articulation between successive lumbar costal plates involves at least three and probably four articular facets. These can be seen only in disarticulated material from which all matrix has been removed. An anteroventral facet (*av f*, Fig. 15B), facing dorsally and slightly laterally, articulates with a posteroventral facet (*pv f*, Fig. 15C) of the next rib plate in front. Between the same two plates there is also a posterodorsal facet (*pd f*, Fig. 15A, B), facing dorsally and slightly medially, which must contact another facet not yet seen because of incomplete or matrix-cemented specimens. The "unknown" anterodorsal facet (*ad f*, Fig. 15A) must occur on the ventral side of the laterally reflected ridge, which is broken off in the specimens in Figure 15B. Since no disarticulated and associated lumbar plates are available, it is impossible to make an accurate estimate of the movements permitted. The small size of the facets is evidence that lateral movements, at least, could not have been great.

Essentially the same mechanism of lumbar rib articulation is known in a Middle Triassic cynodont from Tanzania (see ?*Aleodon*-?*Scalenodon*, BMNH TR.8).

The capitulum and tuberculum of each lumbar rib are conjoined and cannot be distinguished except by position. The neck of the lumbar ribs becomes successively shorter so that the seventh lumbar plate is differentiated closer to the midline than that of the first lumbar. This shift is also augmented by a successive shortening of the synapophyses.

6. THE POSTCRANIAL AXIAL SKELETON OF *DIADEMODON*

MATERIAL. *Diademodon*, the best known gomphodont in terms of cranial morphology and dentition, is in fact poorly known in terms of the postcranial axial skeleton. At present there is only one reasonably complete axial skeleton that can be positively assigned to this genus (USNM 23352). This specimen, of rather friable bone encased in an unusually tenacious matrix, provides a very limited amount of information. Other specimens include *Microgomphodon eumerus* (BMNH R.3581), originally described by Seeley (1895a) and subsequently recognized by Brink (1955) as possibly a juvenile *Diademodon* sp. Broom (1905a) described a single vertebra, apparently from the lumbar series, of a cynodont positively identified as *Diademodon*. Broili and Schröder (1936) gave a fairly complete account of several thoracic and five articulated lumbar vertebrae from a specimen tentatively identified as *Gomphognathus* (= *Diademodon*). More recently Brink (1955) drew up a skeletal reconstruction of *Diademodon*, modeling the postcranial axial skeleton primarily on NMB 531. This particular specimen cannot be positively identified as *Diademodon*, as Brink acknowledged, because it lacks the skull. Furthermore Brink's illustration of the actual fossil does not adequately portray the fact that many features have been reconstructed in plaster or are otherwise lost or obscured. Until more complete and better preserved remains of a positively identified *Diademodon* are available, there is little morphological or comparative data that can be stated with confidence.

MORPHOLOGY. Assuming that NMB 531 is a *Diademodon*, then this genus has at least 30 presacral vertebrae—three more than *Thrinaxodon* and one more than the type of *Cynognathus crateronotus*. The sacrum includes five vertebrae, as in *Thrinaxodon*. Brink (1955: 25) stated that there are only four sacrals in NMB 531, but he overlooked the fact that the rib of the fifth sacral is directed anterolaterally and probably contacted the ilium as in galesaurids. Thus the tail, as preserved in this specimen, has eight vertebrae.

Anapophyses, which are well developed in the cervical series of galesaurids, are apparently lacking in this region in *Diademodon* as they are in *Cynognathus*. Elsewhere they are typically developed. It appears likely that in general morphology and proportions the vertebrae of *Diademodon* are quite comparable to those of *Cynognathus*.

Of particular interest are the costal plates. Brink's (1955) reconstruction of *Diademodon* portrayed the lumbar plates as having a basically galesaurid pattern, i.e., more or less rectangular with a simple imbricating relationship (see Fig. 12C). However USNM 23352, whose generic identity is certain, has lumbar costal plates which are cynognathid in pattern (see Fig. 15). Brink (1955: 25) also states that "the lumbar ribs of *Diademodon* are essentially similar to those of *Cynognathus*." But Brink's reconstruction depicts greater dissimilarity than actually exists. In fact as yet there are no known characters of the lumbar ribs with which to distinguish these two genera. In the middle and anterior thoracic region, however, there is a possible difference between the *Diademodon* and *Cynognathus* rib morphology. In the latter there are either no costal plates or costal plates that are only incipiently differentiated. Brink reconstructs *Diademodon* as having small but nonetheless well-defined costal expansions on all anterior and middle thoracic ribs. The evidence for this in NMB C.531 and in USNM 23352 is equivocal.

7. THE PROBLEM OF EXPANDED RIBS IN CYNODONTS

Critique of Previous Theories

A number of paleontologists have studied cynodont costal plates and speculated upon their functional significance. Their conclusions offer a variety of alternatives. In the following section an attempt is made to evaluate each of the previously proposed theories in terms of the comparative skeletal data presented above.

Seeley (1895b), who originally described *Cynognathus,* did not speculate on the function of the ribs' peculiar morphology except to note that he had not seen any animal, fossil or recent, with a comparable structure.

Gregory and Camp (1918: 540–544) gave a reconstruction of *Cynognathus* and were the first to consider the plates in terms of the living animal. They proposed two hypotheses: first, that "the peculiar characters of the lower dorsal and lumbar ribs are possibly connected with an extremely large size and powerful musculature of the head which might require an equally strong development of axial musculature," and second, that "the sharp differentiation of the dorsal and lumbar region may also indicate that the muscular complex forming the diaphragm [had evolved]." With regard to the first hypothesis, Gregory and Camp do not show why muscular compensation for a heavy head must occur in the lumbar region. In both mammals and reptiles specializations to suspend a large or bulky head invariably occur in the anterior thoracic and cervical regions. This fact considerably undermines the credibility of their first theory.

Gregory and Camp's second theory is more concerned with lumbar and thoracic rib differentiation than with the function of the costal plates. The lack of extensive rib shafts in the abdominal region of cynodonts is an interesting parallel to the mammalian condition and is possibly related to the development of a diaphragm. However this condition cannot be construed as evidence for a diaphragm because there are also reptiles in which the posterior dorsal ribs are either much reduced in size or are represented only by the fused extremities of the transverse processes, i.e., crocodilians. Recognizing the possibility that cynodonts possessed a diaphragm, Gregory and Camp nevertheless do not attempt to relate it to the function of the costal plates. Further criticism of the diaphragm theory is given below with reference to Brink's hypothesis.

Haughton (1924: 90–93), the next author to consider the function of costal plates in cynodonts, unfortunately made no attempt to relate his three hypotheses of costal plate function to his analysis of muscular anatomy. Haughton's first and second hypotheses were that the plates must have added strength to the back and at the same time acted as a protective shield analogous to dermal plates or a carapace. Broom (1932b: 263) also "suspects that a small carapace of fibrous tissue has covered the lower dorsal and lumbar regions." The imbricating arrangement of plates undoubtedly strengthened the back, but Haughton did not elaborate as to exactly how this was accomplished or for what possible adaptation. Cynodont costal plates are hardly analogous to a carapace for, as Haughton himself admitted, the plates probably were covered with well-developed muscles. No dermal ossifications or "carapace" plates have ever been found. While protection may have been a secondary advantage of these plates, there is no evidence to suggest that it was the primary selective factor in their formation.

Haughton's third hypothesis, that the costal plates prevented dislocation during lateral flexure, was based upon the supposition that "more or less sudden bending may have been necessary if . . . [the cynodonts'] food consisted largely of insects." However the interdependence of an insectivorous diet and abrupt lateral flexure of the axial skeleton is by no means established. Certainly not all cynodonts possessing costal plates were insectivorous. Moreover the design of plates did not prevent an animal such as *Thrinaxodon* from assuming a very tightly curled position (Brink, 1958) such as is common among modern mammals when resting. Costal plates therefore could not have acted as a "stop" to prevent lateral flexion. The degree of lateral flexion preserved in the specimen described by Brink is far in excess of what might be reasonably expected in locomotion or in feeding behavior.

Despite the inadequacies of these hypotheses,[8] Haughton's observation that the costal plates possibly served for iliocostalis insertion is of interest, particularly with regard to an analogy drawn by Williston (1925: 115). In his *Osteology of the Reptiles* Williston remarked that the expanded ribs of *Cynognathus* "gave great strength to the lumbar region, and are perhaps analogous to the greatly expanded transverse processes of the crocodiles." The meaning of the last observation is left unexplained, but presumably refers to a lever-like action of epaxial muscles on the long, laterally directed transverse processes. The functional significance of Haughton's and Williston's observations will be considered in following sections.

Brink (1954: 121) proposed that cynodont costal plates developed in conjunction with the evolution of a diaphragm. He elaborated his views with reference to *Diademodon* (1955: 27–28), and again in greater detail with reference to cynodonts in general (1956: 78–84). Brink reiterated Gregory and Camp's (1918) observation that the trunk may be divided into thoracic and lumbar regions on the basis of rib differentiation; the reduction or absence of abdominal ribs permits visceral displacement in response to a contracting diaphragm and is apparently a necessary condition for a diaphragm. However since many reptiles also have reduced ribs or lack them altogether in the posterior dorsal series, thoracolumbar differentiation in mammal-like reptiles is a rather equivocal piece of evidence for a diaphragm. Despite the fact that the presence of a diaphragm in cynodonts is as yet unproven, Brink further speculated that "at this stage the intercostal muscles apparently failed to act as effective antagonists to the diaphragm," necessitating overlapping ribs to maintain the integrity of the thorax. In several respects Brink's hypothesis is untenable. First, the presence of costal plates on *all* presacral ribs in galesaurids is difficult to relate to stresses generated by a diaphragm—stresses which in the cervical and posterior lumbar regions must have been negligible or nonexistent. If costal plates were an adaptation to such stresses, then in later cynodonts (*Cynognathus*, *Diademodon*), in which reduction of the plates occurs, the retention of plates in the thoracic region would be expected. Instead the costal plates of later cynodonts are lost in all thoracic vertebrae except the most posterior and are much elaborated in the lumbar region where diaphragmatic action requires that the visceral cavity be the most distensible. Thus the claim that costal plates arose in response to stresses induced by a diaphragm is supported neither by any biomechanical facts nor by the skeletal distribution of the plates themselves.

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[8] For other criticisms see Brink (1954: 119).

Secondly, there is no evidence to support Brink's (1955: 27) assumption that the intercostal muscles of cynodonts were ineffectual. If indeed the intercostal muscles were inadequate to sustain the intracavitary stresses induced by the diaphragm, the question arises as to why the imbrication of ribs did not extend the entire length of the ribs. Brink's further speculation (1956: 84) that a "largely involuntary diaphragm and fully voluntary intercostal muscles in the Cynodontia could not be brought to well timed cooperation" is without foundation.

Brink's (1955: 27) observation that the lumbar costal plates of *Diademodon* prevented intervertebral rotation is unquestionably valid. Brink further argued that the reduction or loss of thoracic costal plates in *Diademodon* might possibly relate to the necessity of intervertebral rotation, "twisting of the torso" in Brink's terminology, during respiration or locomotion or both. However, even if the costal plate structure is disregarded, intervertebral rotation between dorsal vertebrae of any known cynodont would have been impossible because of the zygapophyseal articulations and the anapophyses. To permit intervertebral rotation, zygapophyses must conform to a radius of a circle, the center of which lies approximately at the nucleus pulposus. In *Thrinaxodon*, *Diademodon* and *Cynognathus*, zygapophyseal orientations in the dorsal vertebral series vary from almost parasagittal to nearly horizontal, thus obviating the possibility of intervertebral rotation. The close fit of each anapophysis into the groove on the next posterior pedicle is another interlocking mechanism which would also prevent rotation. It is difficult to argue convincingly that the prevention of intervertebral rotation, whether during locomotion or respiration, was the prime function of costal plates when the typical adaptations to resist such movements are well developed in the vertebral column.

The Relation of Costal Plates to Epaxial Muscles: A Comparative Review of Epaxial Musculature

The obvious interpretive approach to the problem of an unusual skeletal feature is through reconstruction of non-skeletal anatomy. Muscle patterns and their relation to posture and locomotion are important influences on postcranial bone morphology, and therefore are more likely ~~to be related~~ to an unusual skeletal feature than are other aspects of the soft anatomy.

Cynodont costal plates are located on the proximal half of the ribs, approximately at the point where an angle would be expected. The only supracostal musculature which is continuous along the trunk and neck at this level is the epaxial system. Gregory and Camp (1918) and Haughton (1924) first suggested that the epaxial muscles were involved with costal plates, but failed to explore the possibility. In order to determine the possible distribution of epaxial muscles in cynodonts, a comparative survey of the epaxial muscles in living reptiles and mammals must be made.

THE EPAXIAL MUSCULATURE OF REPTILES

The general plan of reptilian epaxial musculature is tripartite, being divisible into a medial (transversospinalis) system, an intermediate (longissimus) system, and a lateral (iliocostalis) system. Variation can be expected within this basic framework, for reptiles are diverse in habit and locomotion. Some variations reported in classical accounts of reptilian epaxial musculature are merely terminological, while others reflect differences in the detail of dissection. Nevertheless all accounts agree with Vallois' (1922) observation that the transversospinalis, longissimus and iliocostalis systems constitute the basic and primitive reptilian epaxial arrangement.

The transversospinalis system consists of a diverse series of small muscles which are primarily intervertebral but which may also span two or more vertebrae. In *Iguana* (Olson, 1936), for instance, the Mm. interspinalis between adjacent neural spines are inseparable from the Mm. interarcuales between adjacent neural arches. The Mm. interarticulares are distinct, linking adjoining postzygapophyses and having accessory attachments to the prezygapophyses. The Mm. intertransversarii link adjacent transverse processes along their dorsal aspect. The Mm. levator costae, when present in other reptiles, usually arise on the posterior (ventral) surfaces of the transverse processes and insert on the capitular process of the next posterior rib. In *Iguana* these muscles are reduced in size and limited to a few cervical vertebrae.

In addition to short intervertebral muscles there are commonly longer fascicles which span the lengths of two or more vertebrae. These are commonly termed the Mm. spinalis, which arise and insert on the neural spines or their bases and the Mm. semispinalis, which arise on the neural spines but insert either into the dorsal intermuscular septum, separating the transversospinalis and longissimus systems, or into the longissimus system itself. In *Iguana* the Mm. spinalis are represented by a series of small tendons which arise from the base of the spine, pass posteriorly over four vertebrae and insert on the spine of the fifth (Olson, 1936). The Mm. semispinalis arise in continuity with these tendons and insert on the dorsal intermuscular septum.

A primitive or even general pattern of transversospinalis musculature is not easily discerned from available studies of living reptiles. The apparent diversity is no doubt in part due to differences in nomenclature and detail of dissection. However Vallois (1922), in a monographic study of the epaxial musculature of vertebrates, presented evidence that a basic transversospinalis pattern is recognizable in each of the living orders of reptiles, Chelonia excepted. This pattern consists of three distinct groups of fascicles: Mm. spino-articularis, articulo-spinalis and interspinalis. The spino-articularis arises on the zygapophyses and passes posteromedially to insert on a neural spine one or more vertebrae caudal to the origin. The articulo-spinalis runs in the opposite direction; it arises from the zygapophyses and passes anteromedially over one or more vertebrae to insert on a neural spine cranial to the origin. The interspinals, as the name implies, are confined in attachment to the neural spines and also to the neural arches.

The tripartite division of the transversospinalis is somewhat of an oversimplification, as Vallois recognized. Other systems of fascicles, e.g., interarticular and intertransverse muscles, are present in some orders but not in others. Nevertheless there is a basic pattern to the transversospinalis systems and it may best be described in terms of three laminae. The most lateral and superficial system is the articulo-spinalis (sensu Vallois), running anteromedially from zygapophyses to neural spines. Medial and deeper to this is the spino-articularis (sensu Vallois), running posteromedially from zygapophyses to neural spines. Most medial and deepest of all is the interspinalis group; in addition to the interspinal fascicles present in all living reptilian orders, excepting Chelonia, this group may include muscles which span the arches (interarcuales), the zygapophyses (inter-articulars), the transverse processes (intertransverse muscles) as well as the ribs and transverse processes (levator costae). In addition the interspinal group may include specialized derivatives of this system not found in other reptilian orders.

Olson (1936) implied that the medial, posterodorsally directed spino-articularis system[9] is the primitive arrangement, and that the lateral, anterodorsally directed articulo-spinalis system[9] was differentiated later in tetrapod evolution. There is, in fact, no substantial evidence for this claim other than Olson's interpretation of the direction of spinalis and semi-spinalis fascicles in primitive fossil forms. While the muscle scars give evidence of the presence of such fascicles, they do not permit certain interpretation of their direction, i.e., whether anterodorsal or posterodorsal.

It seems likely that the spino-articularis and articulo-spinalis fascicles of the transversospinalis are derivatives of a primitive, metameric epaxial system adjoining the vertebrae. Yet much of transversospinalis system in living reptiles is intervertebral, i.e., between adjacent vertebrae, and thus preserves the primitive, metameric pattern. In general, however, the evolution of the epaxial muscles involves the loss of myoseptal divisions and the development of fascicles spanning many vertebral segments (Vallois, 1922; Olson, 1936). The lateral parts of the reptilian transversospinalis system, i.e., the spino-articularis and articulo-spinalis, participate in this trend and in many reptilian groups may span three or more vertebrae. This trend is still only incipiently developed in reptiles, while in mammals the primitive metameric pattern is thoroughly modified.

The intermediate epaxial group is the longissimus system, and in the trunk it is one muscle, the M. longissimus dorsi. In *Iguana*, as in most living reptiles, this muscle is bounded medially by a dorsal intermuscular septum (Olson, 1936). It takes origin from this septum, as well as from the dorsal edge and medial surface of the ilium, the sacral ribs, and the prezygapophyses of the dorsal vertebrae. It inserts on the transverse processes and proximal rib shafts. The longissimus dorsi is bounded laterally by the lateral epaxial system, the M. iliocostalis dorsi. In *Sphenodon* and most other reptiles, the arrangement is basically the same (Vallois, 1922).

The lateral epaxial group is the iliocostalis system and in the trunk it is a single muscle, the M. iliocostalis dorsi. In *Iguana* this muscle takes origin from the dorsal edge and medial surface of the ilium and by tendons from the M. longissimus dorsi (Olson, 1936). It has a tendinous insertion into the dorsal aspects of the ribs (ibid.). The longissimus dorsi of *Sphenodon* and other reptiles is arranged in a fundamentally similar manner, commonly attaching to intermuscular septa (see Vallois, 1922).

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[9] Olson (1936) referred to these as the spinalis-semispinalis system which has two fiber directions. The difference is only in nomenclature.

THE EPAXIAL MUSCULATURE OF MAMMALS

The epaxial musculature of mammals retains the tripartite arrangement of reptiles. The transversospinalis, longissimus and iliocostalis systems bear similar relationships to each other although individually they display specializations in response to a basically different mode of locomotion.

Slijper (1946: 46; fig. 37) suggested that there is a fundamental difference between mammals and reptiles in the proportions of the transversospinalis and iliocostalis systems. In reptiles the iliocostalis musculature is proportionately larger than the transversospinalis because its lateral position is more mechanically suited to effect the undulatory movements of locomotion than either the longissimus or transversospinalis, which lie medially. In mammals, locomotion involves movement of the spinal column primarily in a sagittal plane and consequently the transversospinalis system is proportionately larger and more differentiated.

Slijper's (1946) comparative data on the epaxial musculature of 80 species of mammals establishes a sound base on which to construct general conclusions about mammalian epaxial patterns, regardless of functional interpretations. The following outline of the mammalian epaxial pattern is based primarily on Slijper's work.

The transversospinalis system, as in reptiles, contains a number of different series of muscles. The terminology of these muscles varies greatly in the literature, largely because the muscles themselves are so diverse in attachment and segmentation that they defy a comprehensive system of classification. The definitions of mammalian transversospinalis muscles given by Slijper (1946: 52) are broadened here so as to include obvious variations. The M. spinalis is a series of fascicles between neural spines and usually spans at least two and usually more vertebrae between origin and insertion. Spinalis fascicles are sometimes intergrown with the M. semispinalis; they originate at the neural spines or a lateral equivalent such as the fascia of the M. longissimus dorsi and pass posteroventrally to the zygapophyses or metapophyses of usually the fourth or more vertebra caudal to the point of origin. The Mm. multifidus, rotatores longi, and rotatores breves are successively more medial (deeper) series which have the same attachments as the M. semispinalis. The M. multifidus spans two, and in some cases three vertebrae, to be inserted into the third or fourth vertebra caudal to the origin. Similarly the Mm. rotatores longi and breves insert into the second and first vertebrae, respectively, caudal of their origin. In addition to these muscles, the M. interspinalis spans the neural spines of adjacent vertebrae as in reptiles. The Mm. intermammillares, or interarcuales of other authors, link adjacent vertebrae by passing between neural arches or metapophyses. Mm. intertransversarii attach to successive transverse processes.

In terms of fascicles connecting major elements or processes of the vertebral column, mammals are not significantly different from reptiles except in one respect. There is a conspicuous absence of semispinalis fascicles running posterodorsally, i.e., from the neural arches or metapophyses posteriorly to the neural spines (Slijper, 1946: 52). The M. semispinalis of mammals runs only from the neural arches or metapophyses cranially to the neural spines.

While the components of the transversospinalis system remain much the same between mammals and reptiles, the arrangement of these components differs considerably. In a few mammals the transversospinalis is undifferentiated throughout the length of the trunk. Semispinalis, multifidus and other shorter fascicles are fused. This occurs primarily in animals with specialized modes of locomotion (Slijper, 1946: 53, table 3) and may be regarded as atypical. For all other mammals it is possible to make two generalizations concerning the transversospinalis system. First, the system tends toward the regional specialization of muscles associated with the thoracic ("prediaphragmatic region" of Slijper) and lumbar ("post-diaphragmatic region" of Slijper) series. This differentiation takes a wide variety of forms, but principally the differences are either in the presence or absence of one or more subdivisions of the transversospinalis, or their fusion into one or more undifferentiated muscle masses (see Slijper, 1946, table 3 for comparative data). Second, the spinalis and semispinalis tend to develop long fascicles which originate in the thoracic and insert in the lumbar region (ibid.: 53–54). Slijper implies—incorrectly—that the differentiation of the transversospinalis system into its various components is a peculiarity of mammals. Reptiles possess muscle fibers which are in basically the same relation to the axial skeleton as are the components of the mammalian transversospinalis system. The primary difference is not that the transversospinalis of mammals is more completely divided into constituent muscles, although this may be true in part, but it is more specialized morphologically in relation to regions of the axial skeleton. This differentiation is reflected in the distinct morphology of mammalian thoracic and lumbar vertebrae, as well as relatively large morphological changes between individual vertebrae. In reptiles the transversospinalis tends to be more uniformly developed throughout the trunk and associated with this is a relatively undifferentiated axial skeleton.

The mammalian longissimus system resembles that of reptiles in its origin from the proximal rib shafts and transverse processes and its partial insertion into the ilium.[10] Here the similarity ends, however. The rest of the inserting fibers tend to displace from the metapophyses to the spinal apices of sacral, lumbar and, more rarely, posterior thoracic vertebrae (Slijper, 1946: 49). This shift probably allows the longissimus to act synergistically with the transversospinalis system, at least with respect to sagittal movements of the lumbosacral region. Furthermore the longissimus is commonly characterized by long fascicles which originate in the thoracic and insert in the lumbar region (ibid.).

The iliocostalis system, with a few specialized exceptions, is relatively narrower and smaller in mammals than in reptiles (Slijper, 1946: 46). Like the longissimus system, it characteristically has long fascicles but may, in the thoracic region, retain shorter fascicles which approximate a metameric condition (ibid.). In particular the iliocostalis tends to separate into an M. iliocostalis thoracis and an M. iliocostalis lumborum. The latter is usually found to be fused in a variable degree with the longissimus by means of a dense, sheet-like aponeurosis extending from the midline laterally over the dorsal area; the combined musculature is known as the M. erector spinae. This arrangement is a further development of the mammalian trend to develop musculature for sagittal movement or fixation of the spinal column.

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[10] Slijper (1946: 49) incorrectly stated that the reptilian longissimus dorsi does not insert on the ilium. For numerous examples that contradict this assertion, see Maurer (1899), Romer (1922b) and Olson (1936).

The foregoing review of epaxial muscles in living reptiles and mammals has emphasized that the two classes share a common tripartite pattern of back musculature. In reptiles much of the primitive, metameric pattern is retained despite specializations and the tendency to parallel the mammalian development of longer fascicles. Associated with their comparatively primitive myology is a relatively undifferentiated axial skeleton. The iliocostalis is commonly the largest of the epaxial muscles, a correlate of locomotion involving lateral undulation. In mammals the axial skeleton is highly differentiated and so also is the epaxial musculature. The transversospinalis is well developed and, together with the specialized erector spinae, contributes to the ability to effect sagittal movements important to locomotion. With these considerations in mind, it is now possible to make a functional evaluation of the axial skeleton of *Thrinaxodon*.

Reconstruction of the Epaxial Musculature in Thrinaxodon

In living reptiles and mammals the epaxial musculature is tripartite and it may be confidently assumed that the arrangement was similar in *Thrinaxodon*. The most medial of the three, the transversospinalis system, will be considered first.

The transversospinalis of *Thrinaxodon* was probably confined, as in living tetrapods, to the space medial to the distal ends of the transverse processes. The repetitious uniformity of the dorsal vertebrae is evidence that this muscular system was more similar to the reptilian than to the mammalian pattern. In mammals many of the components of the transversospinalis are restricted to or are differently developed in various segments of the spinal column. This is associated with functional differentiation of vertebral regions (thoracic, lumbar, etc.) as well as with rather sharp morphological gradients between adjacent vertebrae. No such differentiation is evident in *Thrinaxodon*. Thoracic and lumbar vertebrae are remarkably uniform. In lateral aspect the spines and arches form smooth, non-angular surfaces which are not interrupted by large metapophyses or muscle scars. The undifferentiated vertebral morphology is evidence that the muscular structure retained a primitive metameric pattern. Moreover the neural spines are relatively short and thus provide neither the height nor the leverage for a strong transversospinalis system capable of producing effective sagittal flexure.

In *Thrinaxodon* the Mm. interarcuales and interarticulares were probably not differentiated because their areas of attachment are smoothly confluent. Minute metapophyses on the postzygapophyses of the dorsal vertebrae (*m*, Fig. 12A) indicate that the Mm. interarticulares may have been partly tendinous. The anterior margin of each dorsal neural spine, except those of the first two thoracics, extends nearly to the posterior margin of the next vertebra. The anterior margin, being extremely thin, is frequently broken, but in several fairly complete specimens it is clear that the anterior margin of each neural spine was accommodated in a vertical recess in the posterior margin of the preceding spine. There was obviously no contact between adjacent spines, but the extremely close proximity effectively prevented any extensive sagittal flexion. As a result the M. interspinalis in the thoracolumbar region was probably poorly developed and perhaps entirely replaced by an interspinous tendon.

The Mm. Levator costae, running from the posteroventral aspect of the transverse processes to the next posterior rib, were probably well-developed. The insertions on the anterior aspect of the shafts between the capitulum and tuberculum are marked by rugosity and a slight tuberosity or crest. The probable area of origin lies on the posteroventral surface of each transverse process and on the continuation of this surface onto each tuberculum. Together these surfaces form a concavity which becomes progressively deeper posteriorly (*cp*, Fig. 12B). The concavity bears a moderate amount of rugosity, especially along its dorsal rim. The development of large Mm. levator costae, as interpreted from these areas of attachment, relates to the production of lateral flexure of the vertebral column. With the ribs fixed either by synostosis with the vertebrae, in the lumbar series, or by union of the costal cartilages to the sternum, in the thoracic series, tension between transverse processes and ribs would tend to cause rotation of the vertebrae, and hence lateral flexure of the column. It is certain that the Mm. intertransversarii between adjacent transverse processes could have produced such movement and it is probable that the Mm. intertransversarii and levator costae were closely associated functionally if not actually a single muscle mass. Therefore the most strongly developed part of the transversospinalis system in *Thrinaxodon* is situated to produce lateral, not sagittal, movements of the vertebral column.

It is possible that the transversospinalis muscles associated with the cervical and first four thoracic vertebrae were more differentiated than the simple, metameric muscles of the trunk. The elongate, narrow spines of these vertebrae differ from each other in the degree of recurvature and apical thickness. Such variation is evidence of differences in stress and muscular attachment. Their height permits deeper and hence stronger transversospinalis musculature than in the thoracolumbar region. Both height and recurvature provides advantageous leverage for Mm. multifidus and rotatores, as well as for the longer spinalis or semispinalis musculature. In most reptiles, however, the cervical vertebrae are in some degree modified by the special requirements of suspending the head and both the transversospinalis and longissimus systems tend to develop long fascicles. The differentiation of cervical vertebrae in *Thrinaxodon* cannot be considered as a strictly mammalian feature because both reptiles and mammals respond to the problem of head suspension by specialization of the cervical vertebrae and muscles. Nevertheless, with the possible exception of the anterior thoracic and cervical regions, the transversospinalis system of *Thrinaxodon* appears to have retained the primitive, basically metameric structure of a reptilian grade.

In *Thrinaxodon* the longissimus system occupied a wide, parasagittal trough along the dorsal aspect of the axial skeleton, an interpretation shared with Haughton (1924) and Brink (1954). This trough is bounded medially by the neural spines (or transversospinalis musculature during life), ventrally by the transverse processes and ribs, and laterally by the upturned costal tubercles. Its position is analogous with the longissimus position among most living tetrapods in which, of course, no trough is developed. The "floor" of the trough is discontinuous by virtue of the intercostal spaces. It is deepened laterally by the emargination (*gr*, Fig. 12A) of the dorsal aspect of the rib shafts. In the posterior lumbar vertebrae the transverse processes are also emarginate distally, thus broadening the trough near the sacrum. Emargination of sacral ribs is well-developed on the first two, less developed on the third and fourth, and absent on the fifth. The development of the trough is explicable in terms of providing space for an enlarged M. longissimus dorsi. If, as in living reptiles and mammals, the longissimus system in *Thrinaxodon* took origin from the sacrum, from the medial surface and dorsal edge of the iliac blade, and from the transversospinalis fascia, then this musculature must have been relatively well developed because these surfaces are extensive. The likely points of insertion—the transverse processes and medial surfaces of the costal tubercles—also form an extensive surface area which is consistent with a large muscle mass. The grooved dorsal surface of the ribs medial to the costal tubercles appears to have accommodated the belly of the longissimus from which inserting slips may have branched on either side. It appears probable that the longissimus system in the trunk was composed of a single, non-segmented muscle mass. Metameric segmentation, if present, would have been delineated in part by tendinous myosepta (myocommata) for which there is no evidence (for evidence of myosepta in fossil forms, see Olson, 1936). Furthermore, metameric segmentation would not account for the emargination of the ribs which creates a continuous trough from the sacrum to the anterior thoracic vertebrae.

The M. longissimus dorsi as interpreted in *Thrinaxodon* is a well-developed muscle running the length of the trunk. Unilateral contraction of this muscle would laterally flex the spinal column. The efficiency of such action was apparently augmented in the lumbar region by fusion of the ribs to the transverse processes. Lumbar ribs act as extensions of the transverse processes and are analogous to lateral levers. In mammals, for instance, the neural spines are lengthened to function more efficiently as sagittal levers (Slijper, 1945: 79 ff.). The principle is the same in *Thrinaxodon*, except the levers are arranged to transmit lateral forces.

The transition from mobile to immobile ribs is in the posterior thoracic vertebrae. The efficiency of mobile ribs as levers was probably diminished only slightly because the capitulum and tuberculum are robust structures and retain extensive contact with the vertebrae. Furthermore the capitulum is located anteroventral to the tuberculum. This arrangement would permit rib movement anterodorsally or posteroventrally, with the center of the capitulum and tuberculum acting as hinge points. However, the overlapping costal plates prohibit such movement and therefore eliminate the only possibility for significant rib movement independent of the vertebrae.

In the anterior thoracic series the longissimus trough is narrower, suggesting that here the muscle was smaller and lateral flexure perhaps less extensive. The capituli and tuberculi of anterior thoracic ribs lie in a more or less vertical relationship and the costal plates are nearly vertical. This arrangement would permit limited costal movement, probably associated with respiration, if the distal ends of the shafts were not immovably joined to the sternum.

The iliocostalis system, the most lateral of the epaxial musculature, probably occupied the external (dorsal) surfaces of the costal plates in the trunk and neck. As is common in most tetrapods, its extent would be interrupted by the ilium, although the more medial longissimus system might be continuous over the sacrum into the caudal series. The caudal iliocostalis system was probably represented by the lateral part of the M. extensor caudae lateralis, as in *Iguana* (Olson, 1936).

There is no osteological evidence as to whether the M. iliocostalis dorsi was a series of metameric muscular bundles between adjacent costal plates or was a single belly with multiple attachments. Metamerism of the trunk iliocostalis is retained by many living reptiles (Vallois, 1922). Whatever the particular arrangement in cynodonts, the size of the costal plates is evidence that the M. iliocostalis dorsi was well developed and probably the strongest of the epaxial systems. The insertions on the costal plates were most likely limited to the posterior margins of the plates, which are slightly swollen, and the bulbous costal tubercles. The remainder of the dorsal surface was probably free of muscle fiber attachment because during lateral flexure this area appears to have been rather snugly covered by the next adjacent plate.

The second and third cervical ribs of monotremes possibly represent morphological derivatives from a cynodont pattern. In *Ornithorhynchus* the axis bears a flat, platelike rib (*r*, Fig. 7; cf. Lessertisseur and Saban, 1967: fig. 348) which apparently persists freely articulating throughout life. The axis rib resembles in general form the expanded proximal ends of the cervical ribs in *Thrinaxodon* (see p. 57) although distally it lacks an attenuating shaft. The third cervical rib resembles the axis rib but is smaller and synostoses with its vertebra to form a very elongate transverse process. Remaining cervical ribs, also fused, are more comparable to transverse processes typical of mammalian cervical vertebrae. The caudally directed axis rib overlaps and contacts the third cervical rib. A synovial joint appears to be developed at the point of contact. Imbrication and intercostal joints are principle features of cynodont rib specialization and the association of these features in *Ornithorhynchus* is possibly a retention rather than a parallel development. The morphology of *Tachyglossus* cervical ribs is similar except that the axis rib is also synostosed. Virchow (1929) reported that the major muscular attachments to the axial rib in *Ornithorhynchus* were the rectus capitis lateralis and the so-called spinotransversalis cervicis. The homology of the latter muscle is in doubt. Its continuity with the iliocostalis might suggest derivation from this group. Such an interpretation would be consonant with the hypothesis that cynodont rib plates were related to the iliocostalis group. However, Virchow concluded that the spinotransversalis cervicis is a specialized derivative of the longissimus, which in cynodonts probably lay immediately medial to the rib plates. Vallois (1922) claimed that in *Tachyglossus* the longissimus attaches to the cervical ribs but here also there is doubt as to the homology. The function of these ribs in monotremes should be investigated.

The Possible Functions of Cynodont Costal Plates

The association of an apparently well-developed iliocostalis muscle with costal plates must have been functional. Unfortunately the analogous condition has never evolved in any other fossil or living group, although the expanded ribs of certain modern edentates are probably comparable to a degree. Two functions of the axial skeleton which are most likely to have been related to the development of costal plates are locomotion and posture. Locomotion will be considered first.

The comparative study of Vallois (1922) shows that among living reptiles the lateral system, the iliocostalis, is relatively larger than in mammals. Moreover Vallois established that the iliocostalis usually comprises the greater part of the reptilian epaxial musculature, the exception being that in Chelonia the epaxial system of the trunk is vestigial and undifferentiated. Obviously these facts are related to a mode of locomotion in which lateral flexure of the trunk is an important mechanism for advancing the limbs. Slijper's observation (1946: 44) that ribs act as levers which effect these movements is fundamental to understanding the basic mechanism of such locomotion. The efficiency of lateral flexure per unit of muscular contraction varies with the distance from the axis of flexure, i.e., from the vertebral column. Semispinalis fibers of the transversospinalis system, for example, have a short moment arm with respect to the vertebral axis, while fibers of the more lateral longissimus system have a relatively longer moment arm. Assuming that the contractile properties of these muscles are equal, the transversospinalis is less efficient than the longissimus in producing lateral flexure. Gans and Bock (1965) review various factors which invalidate this assumption. However the question here is one of simple mechanics, without reference to the relative efficiency of the energy (muscles) involved. The transversospinalis produces a greater degree of lateral flexure per unit of contraction, which means that it is more advantageously located, all factors being equal, to produce rapid flexing movements. The iliocostalis, the most laterally situated of epaxial musculature, occupies the most mechanically advantageous position to effect lateral flexure. In cynodonts this muscle could have been hypertrophied to generate a great amount of muscular power at a mechanically efficient position. The result, of course, would emphasize a reptilian rather than a mammalian mode of locomotion. In view of the fact that the appendicular anatomy retained so many primitive characteristics, it is perhaps not surprising that locomotory specialization should occur in the axial skeleton.

To account adequately for morphological details of the costal plates would require knowledge of the precise arrangement of the iliocostalis. Even so, the costal plate series shows a morphological gradient that could be studied functionally only in the living animal. Nevertheless a few speculative deductions may be made on the basis of osteological evidence alone.

The initial impetus for costal plate formation may have resulted from the fact that a convex flange increases the insertional area. A sharply curved posterior border unquestionably provides a longer linear surface than does the comparable length of a normal rib shaft. The costal tubercle, reflected dorsally so as not to impinge upon the adjacent longissimus, may have been an extension of this insertional area.

If a costal plate is examined on its ventral side, the ridge which represents the original rib axis, or shaft, passes near the anterior edge of the plate (Figs. 13D, 16). Therefore the bulk of costal plate expansion has taken place posteriorly. The effect has been to move the iliocostalis insertion also posteriorly (from *A* to *B*, Fig. 16). The lever arm of a posteriorly directed iliocostalis force (*F*) is the same if the muscle inserts at point *B*, as in cynodonts, or at point *A* as is the usual condition among other tetrapods, for the displacement due to plate expansion is more or less perpendicular to the lever arm.

However, there is another force generated by the iliocostalis which in certain positions of the spinal column may assist lateral flexure. This force results from the tendency for a non-linear elastic body to straighten itself during flexion. In other words, the iliocostalis tends to assume the position of the vertical dotted line in Figure 16. As

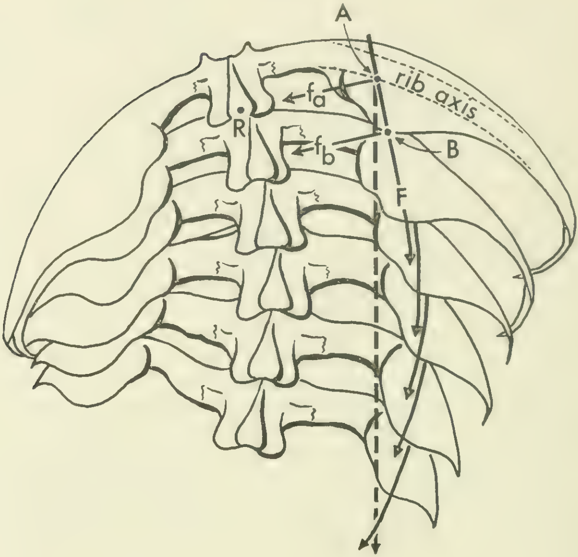


FIG. 16. Diagrammatic representation of six thoracic vertebrae and ribs of *Thrinaxodon* to illustrate the possible effect of iliocostalis force (F) applied at the edge of a costal plate (B). The iliocostalis, initially acting along an arc, tends to straighten itself to the heavy dashed line. In so doing it generates a medially directed force (f_b) at point B. The force f_b has a moment arm of AB length with respect to rotating the vertebra about point R. If the iliocostalis inserted on a normal rib at point A, the analogous force f_a would have no rotational lever arm with respect to rotation at R.

the muscle contracts, it not only increases the overlap between ribs but also exerts a medial force against its points of insertion. If the insertion (A) is directly lateral to the axis (R) about which a vertebra rotates during lateral flexure, no additional rotational effect is achieved. Instead, the force (f_a) is dissipated on the intervertebral disk and ligaments. If, however, the insertion of the muscle is displaced posteriorly (B), the medially directed force (f_b) gains a lever arm with respect to the vertebra and tends to rotate the vertebra about its axis. In cynodonts the insertion is displaced posteriorly by the caudal extension of a costal plate, with a resultant lever arm length A-B of force (f_b). Hence muscular energy is retained which otherwise would not be directed toward effecting flexure of the spinal column. The fact that costal plates form a continuous surface through imbrication ensures that these forces are utilized even at points of muscle-rib contact where there is no actual insertion.

The inherent deficiency of any hypothetical analysis that treats rib plates as muscular processes lies in the failure to account for the diversity in morphology and distribution of these plates. If a single, fundamental feature common to all rib plates is sought, the obvious characteristic is overlap or imbrication. In simplest functional terms, costal overlap gives one vertebral segment additional support by an accessory contact with the next. The possible importance of axial strength to cynodonts may have involved certain evolutionary "experiments" in posture.

Postural differences between reptiles and mammals involve features which are either mutually exclusive, e.g., the orientation and excursion of the humerus is consistently different between the two classes, or differ in the degree to which they are employed. For example, rapidly moving crocodilians will elevate the trunk well off the ground and arch the spinal column (cf. Schaeffer, 1941b: 391; Colbert, 1948: fig. 22); this behavior approximates a mammalian posture. The critical difference, however, is that crocodilians do not sustain this posture for more than a short time and are probably physiologically incapable of doing so. Costal plates in cynodonts may have represented an "experiment" in musculoskeletal adaptation to sustain a more mammalian posture. It seems plausible, at least, that a structural adaptation for mammalian posture may have preceded or evolved concomitantly with the complex of physiological adaptations for sustained activity.

Cynodont costal plates would have provided intrinsic strength to the vertebral column, regardless of the associated musculature. The imbrication of successive ribs is a simple mechanism to ensure axial support and thus to maintain a posture in which the trunk is held off the ground. I have shown that the anteroposterior expansion of ribs among certain living edentates probably may be related to thoracolumbar stability (Jenkins, 1970b). This stability is employed in digging (*Myrmecophaga*, *Tamandua*) when the trunk and hind feet serve as a stable base for the powerful forelimb stroke. In the Least Anteater (*Cyclopes*) thoracolumbar rigidity is employed in arboreal locomotion; with the hind feet and prehensile tail grasping a branch, the rest of the body is stretched out to reach an adjoining branch. This maneuver is believed to be accomplished in part by virtue of the overlapping ribs. The intercostal muscles "lock" one rib against another, thus forming a trunk so rigid that it can remain in a horizontal position without support of the forefeet. Obviously the overlapping costal plates of cynodonts do not represent a parallel fossorial or arboreal specialization. But certainly the effect was analogous. Whether the increase in intrinsic vertebral column strength was a locomotory or postural adaptation, as here suggested, or due to some other habitus factor cannot be established at present.

The phylogenetic distribution of cynodont costal plates is another aspect of the problem. The earliest known cynodonts, e.g., *Leavachia*, from the *Cistecephalus* zone, apparently possessed normal, unexpanded ribs (see Jenkins, 1970a, for a possible exception to this point). By *Lystrosaurus* zone times cynodonts such as *Thrinaxodon* developed costal expansions on all presacral ribs. During the Middle Triassic, which saw the last of cynodonts in any abundance, expanded ribs are found typically in the most posterior thoracic and lumbar region. In *Cynognathus*, however, there is evidence of a slight costal expansion on the axis rib and to a lesser degree on the sixth and seventh cervical ribs. The tendency toward reduction of rib specialization is particularly well documented among South American traversodontids (Bonaparte, 1963a; Jenkins, 1970a).

Both diademodontids and cynognathids, which are quite divergent in cranial morphology and particularly in dentition, elaborate the interlocking mechanism between the lumbar rib plates (see above, p. 73). Morphologically both the lumbar and posterior thoracic ribs appear to be very similar among representative Middle Triassic genera; the scant material available from *Cynognathus* (BMNH R.2571; UCMP 42729) and *Diademodon* (NMB 531, USNM 23352), at least, shows no significant differences. The paradox is that galesaurids, with the most extensive development of costal plates, precede Middle Triassic cynodonts in which only the posterior dorsal ribs bear the characteristic modification. If the galesaurid pattern is ancestral to the cynognathid-diademodontid pattern, then a reduction of this feature occurred, except in the lumbar series where it was further elaborated. If, on the other hand, Middle Triassic cynodonts were not derived from a galesaurid with a full complement of expanded ribs, then the question arises as to what extent are similarities due to common ancestry or parallel evolution. Were cynodont phylogeny better known, the course and perhaps the adaptive factors of costal plate evolution would be more apparent.

Whatever the evolutionary course of costal plates, certain tentative deductions may be made from their distribution and morphology among the most advanced cynodonts. In these forms costal plates are restricted to the posterior dorsal region and are absent or little developed elsewhere. Their retention and further elaboration in the "lumbar" region is perhaps indicative of their functional suitability to resist structural weakness in this area.

As a general rule the lumbar region among mammals is reinforced by several features not found elsewhere along the column. Lumbar centra are commonly the most massive of all centra. The lumbar column is further stabilized by a strong M. erector spinae, representing the fused Mm. longissimus and transversospinalis systems. The thoracolumbar aponeurosis, usually thickest in the lumbosacral region, represents a sturdy attachment for erector spinae fibers. Furthermore the lumbar column is supported by subvertebral muscles, the M. psoas major (from lumbar vertebrae to femur) and M. psoas minor (from lumbar vertebrae to ilium). All these features are attributable, at least in part, to the fact that the lumbar column must transmit the hind feet thrust forward against the inertia of a large percentage of body weight. In addition the lumbar region in many mammals is an area of significant mobility. Yet this region lacks ribs, and thus the possibility of muscular attachment thereto, which would contribute to its ability to withstand both intrinsic, i.e., weight, and extrinsic, i.e., locomotory thrust, forces. In edentates of fossorial habitus xenarthrous vertebrae occur in the lumbar and posterior thoracic region; this feature apparently contributes to lumbothoracic rigidity, or "body bracing", during fossorial activity (see Jenkins, 1970b). Another not uncommon adaptation to reinforce the lumbar region is to shorten it altogether.

In cynodonts the typical mammalian adaptations for lumbar support were apparently not developed, or at best were only incipiently developed. Lumbar centra are slightly longer and not significantly wider than anterior dorsal centra; the degree of differentiation is not greater than that found among living reptiles. For reasons given above (see pp. 83-86), cynodont epaxial musculature is believed to have retained a primitive tripartite arrangement and probably did not develop a true M. erector spinae and thick thoracolumbar aponeurosis as in mammals. Furthermore, it is very likely that cynodonts had not yet developed a mammalian arrangement of psoas muscles. Romer (1922b: Pl. XLV) reconstructed the homologues of these muscles in

Moschops as arising from the pubis, which is the primitive, reptilian origin. For reasons given below (see p. 181) it appears that this muscle mass in cyndonts was similarly disposed. Dorsal migration to a mammalian position had not yet occurred. Thus an M. psoas minor could not have been present to aid in fixation of the lumbar series.

The absence of lumbar specializations typically associated with a mammalian posture does not constitute proof that costal plates were a primitive adaptive substitute. However, if advanced cynodonts were making certain physiological advances toward mammalian behavior, then it is reasonable to expect that the musculoskeletal system should have responded to the stresses induced by such activity. Certainly the lumbar region, together with the pelvis, underwent profound changes in the therapsid-mammalian transition in response to a basic functional reorientation; costal plates may well represent an early manifestation of the selective processes which eventually formed the mammalian pattern.

PART TWO. APPENDICULAR SKELETON: PECTORAL GIRDLE AND FORELIMB

1. PECTORAL GIRDLE

SCAPULOCORACOID (Figs. 17–21)

MATERIAL. The cynodont shoulder girdle is composed of a scapula, coracoid, procoracoid, clavicle and interclavicle. A cleithrum is not present. In no cynodont is a complete, associated shoulder girdle known. However numerous specimens of *Thrinaxodon* (AMMM 5265; NMB C.392; SAM K.1395; and USNM 22812, among others) provide an adequate picture of the morphology of separate elements. In addition incomplete scapulocoracoids are known in *Cynognathus* (BMNH R.2571; UCMP 42729). Broom (1909) gave a brief description of a *Cynognathus* scapulocoracoid, clavicle and interclavicle, but the specimen is not figured and cannot be located. Brink (1955) described and figured a scapulocoracoid (DMSW 224) which he identified as *Diademodon laticeps*; however for reasons already made clear (see footnote, p. 13) both generic and trivial identifications are in doubt. Two collections (BPI 1675; NMB C.2698, C.2700, C.2711) in which disassociated remains of *Cynognathus* and *Diademodon* have been intermixed show that the shoulder girdle elements of these genera are extremely similar and cannot be distinguished, presently at least, without diagnostic cranial material. Indeed the morphology of shoulder girdle elements of *Thrinaxodon*, *Cynognathus* and *Diademodon* is so uniform that a single description suffices; persistent minor variations are mostly due to differences in ossification. The girdles of other cynodonts are either unknown or are too fragmentary to permit reliable comparison.

The scapula of *Galesaurus* is known from a very incomplete specimen (SAM K.1119) and another specimen (UMC R.2722) which is rather complete but is not certainly identified as belonging to this genus.

The poorly preserved scapulocoracoid of *Glochinodontoides* (TM 83) described by Haughton (1924) is only tentative confirmation of its similarity to the scapulocoracoid of other cynodonts.

A partially prepared specimen of *Leavachia* sp. (BPI 374) and the type of *Leavachia duvenhagei* (RC 92, described by Broom, 1948: 618 627 and again figured by Brink and Kitching, 1953a: 315) indicate the procynosuchid girdle is essentially the same as that of any other family of South African cynodont. Neither specimen is completely prepared, however. Brink and Kitching's figs. 1 and 2, made after further preparation has been undertaken on the type specimen, shows that Broom's fig. 40 is a largely hypothetical reconstruction of the coracoids. Without complete preparation of existing specimens or the recovery of new material the pectoral morphology of *Leavachia* must remain somewhat in doubt.

Owen (1876: 21) briefly described the coracoids in *Cynochampsa laniarius*, a genus considered questionably synonomous with *Diademodon* by Watson and Romer (1956: 65). These specimens, numbered S.A. 42 and S.A. 43, were presumably part of the British Museum (N.H.) collection, but could not be located for study.

MORPHOLOGY. The scapula is markedly bowed laterally and bears a high, narrow blade, the vertebral border of which is anteroposteriorly expanded. However the greatest surface area is found across the middle of the blade where the sharp lateral flexure of the cranial and caudal borders forms a narrow but deep fossa for the M. supracoracoideus (*f spc*, Figs. 17A, 18A). This muscle, generally considered to be the homologue of the mammalian spinati, was probably most strongly developed where the fossa is deepest, i.e., across the middle of the scapular blade. Therefore it is possible that its dorsal migration was as yet incomplete (cf. Gregory and Camp, 1918: 511; Romer, 1922b: 532ff.; Jouffroy and Lessertisseur, 1967: fig. 10). The supracoracoideus fossa does not extend ventrally to the glenoid but terminates as a narrow, open groove well up on the blade (*gr*, Fig. 18A); from this groove the muscle, perhaps in part or wholly tendinous, ran to its insertion on the greater tuberosity. The caudal border of the scapula extends to the edge of the glenoid as a clearly defined crest, although at the scapular base it is merely a low ridge and not a free flange of bone as along the cranial border. The flange of the cranial border continues to the scapular-procoracoid contact as a thin sheet of bone. Ventrally, however, the cranial border is everted so that it is directed anteriorly instead of laterally (Figs. 17C, 18C). This part of the scapula appears to have been very thin and in only a few known specimens is it preserved in nearly complete condition. Apparently the clavicle articulated with the scapula here, but this articulation is not well preserved in any known specimen.

An acromial process appears not to have been developed in *Thrinaxodon*, for in excellently preserved specimens the everted edge is extremely thin and apparently complete. In the best preserved specimens a localized thickening occurs on the dorsal half of the everted edge and this may represent the point of acromioclavicular articulation (*?acr*, Fig. 18C). In *Galesaurus* Broom (1932b: 279) claimed that the acromion "is merely a fold on the anterior edge of the bone." In *Cynognathus crateronotus* (BMNH R.2571) there is a robust acromial tuberosity protruding anteriorly from the dorsal half of the edge (Seeley, 1895b: 93; see also Broom, 1909). A similar acromion apparently occurs in *Diademodon* (Brink, 1955: 28), although in most known specimens (*acr*, Fig. 17C) it is invariably damaged or lost.

An anteroventral division of the M. supracoracoideus probably originated in the two shallow concavities along the adjacent anterior borders of the scapula and procoracoid (*spc*, Fig. 19F). Such an arrangement might represent an early stage in the differentiation of the mammalian infra- and supraspinatus muscles (for a brief review of various opinions as to the reptilian homologues of the Mm. spinati, see Romer, 1922b: 532 ff. and Howell, 1937b). However it is improbable that the anteroventral

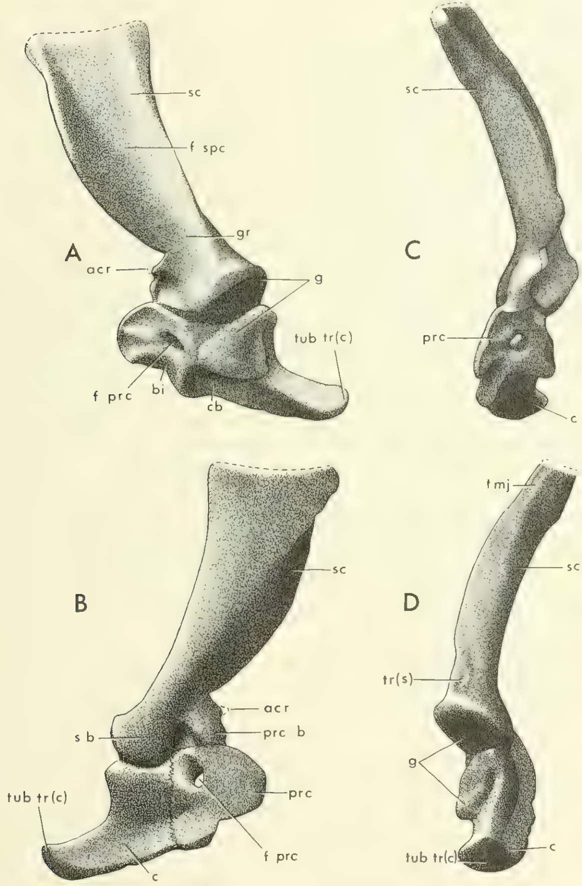


FIG. 17. Left scapulocoracoid of cf. ?*Cynognathus* (?*Diademodon*), NMB C. 2711. A, lateral; B, medial; C, anterior; D, posterior views. The acromion has been broken off and is restored (dashed line) in A and B. The vertebral border of the scapula has likewise been restored; in life the scapula was probably extended by a cartilaginous suprascapula, not shown. X0.4. Abbreviations: *acr*, acromion process; *bi*, fossa for origin of biceps muscle; *c*, coracoid; *cb*, fossa for origin of coracobrachialis muscle; *f prc*, procoracoid foramen; *f spc*, supracoracoid fossa homologous with mammalian infraspinatus fossa; *g*, glenoid; *gr*, groove marking ventral termination of supracoracoid fossa; *prc*, procoracoid; *prc b*, procoracoid buttress; *s b*, supraglenoid buttress; *sc*, scapula; *t mj*, groove presumed to represent teres major origin; *tr* (*s*), shallow groove presumed to represent scapular head of triceps origin; *tub tr* (*c*), tuberosity for origin of coracoid head of triceps.

division of the supracoracoideus had any fibers running beneath the clavicle to the medial surface of the scapula, thus functioning as a true supraspinatus; the flange extends so far anteriorly that fibers passing to the medial surface would turn an angle of at least 180°. On this basis Romer (1922b: 535) argued against the possibility of a mammalian supraspinatus in *Cynognathus* and the argument is equally valid for all other cynodonts in which the scapulocoracoid is known. Yet Sukhanov (1961) found that in the agamid *Phrynocephalus mystaceus* a supracoracoideus fascicle passes beneath the clavicle and around the anterior border of the scapula to attach to the medial scapular surface. In reaching this surface the fascicle must turn an angle of approximately 180°. The muscular arrangement that Romer believed to be theoretically improbable is in fact possible. Nevertheless the relatively large size of the cynodont procoracoid and its close apposition to the clavicle appears to have blocked any supracoracoideus fibers from passing beneath the clavicle to the medial scapular surface (see frontispiece). To open a route for supracoracoideus migration either the acromioclavicular articulation must displace relatively dorsad, as in *P. mystaceus*, or the procoracoid must be reduced. Coracoid reduction seems to have been a principal factor in the evolution of the mammalian supraspinatus and may have initially involved the development of fenestrae; the cynodont coracoid is already sculptured by fossae. An analogy may be drawn with the fenestrae in the scapulocoracoid of *Iguana* that encircle the origins of the Mm. supracoracoideus, biceps and scapulo-humeralis anterior (Fig. 19E).

Monotreme shoulder musculature has undoubtably specialized to some degree and should not be interpreted a priori as a "prototherian" prototype. This point is well exemplified with reference to the spinati. Howell (1937a: 203–204), in a classic comparative study, investigated the possibility of an infra- and supraspinatus in monotremes and concluded that precise homologues could not be determined. He wrote that:

> It is extremely likely that in the broad sense these muscles [i.e., the coracohumeralis intermedius and profundus, which, in Fig. 19G, are indicated simply as supracoracoideus] of monotremes represent mm. supraspinatus, infraspinatus, and possibly the anterior part of subscapularis of placentals, but it cannot be stated without reservation that the deepest division of the former sort of mammal represents any particular one of the three muscles of the latter sort. . . . In this connection it must be remembered that the monotremes are very much specialized, and that in them suprascapular musculature, although definitely suggested, apparently has been arrested far short of the conditions indicated in Permian dicynodonts, or even some of the cotylosaurs. Accordingly the precise arrangement of the deeper coracoid musculature that finally gave rise to true suprascapular musculature may have been quite different from that now encountered in monotremes.

Even on the assumption that monotremes retain a semblance of a therapsid muscular arrangement, the major obstacle to interpreting cynodont shoulder musculature on the basis of the monotreme pattern is the dissimilarity of cynodont and monotreme scapulae. Details of this dissimilarity will be discussed with reference to individual muscles.

The caudal border of the cynodont scapular blade extends from the vertebral border to the upper rim of the glenoid and represents a division between medial and lateral aspects of the scapular blade. The caudal border is here interpreted to represent a division between the area of attachment of the subcoracoscapularis and scapular triceps muscles medially and the supracoracoideus and teres muscles laterally.

In larger cynodonts, especially those represented in the BPI 1675 collection, a vertical, linear depression occurs on the lateral aspect of the scapular blade immediately above the glenoid rim and adjacent to the caudal border. This feature, facing posterolaterally, may represent the origin of a teres minor (*t mn*, Fig. 19F). The scar is not found in all cynodont scapulae and is invariably absent in smaller species in which ossification is generally less complete. Romer (1922b: 532) believed the M. scapulo-humeralis anterior of reptiles to be the homologue of the mammalian teres minor. However Howell (1937b), followed recently by Jouffroy and Lessertisseur (1967), argued convincingly that the teres minor is a derivative of the reptilian M. dorsalis scapulae and therefore primitively associated with the deltoid. Cynodonts offer no evidence for either of these alternatives. Whether a derivative of the scapulohumeralis anterior or the deltoid, the mammalian teres minor must have undergone posterior migration to reach its characteristic position along the caudal border of the scapula.

The teres minor as here reconstructed in cynodonts is positioned essentially as a mammalian teres minor. Gregory and Camp (1918: 471) gave a similar reconstruction for this muscle in *Cynognathus* although they illustrated the origin as being slightly more anterior. The present interpretation aside, the question remains whether the teres minor differentiated before or after the scapular invasion of the supracoracoideus. The position of the large teres minor and relatively undifferentiated supracoracoideus in monotremes (as identified by Howell, 1937b, and Jouffroy and Lessertisseur, 1967) is suggestive of the former. This possibility is based on the assumption that the basic arrangement of monotreme shoulder musculature is primitive for mammals—an assumption which cannot be supported by direct evidence at present. The teres minor of monotremes occupies a position analogous to that of the groove on cynodont scapulae which I have interpreted as the supracoracoideus origin (see above). Thus the cynodont scapular groove may represent a teres minor rather than a supracoracoideus origin.

In cynodonts the scapular head of the triceps took origin from the medial surface of the scapula adjacent to the caudal border. This surface faces posteriorly and in many specimens bears a shallow groove which presumably marks the origin [*tr*(*s*), Figs. 18D, 19F]. The groove is variably developed and in the larger cynodonts it is often scarcely discernible [*tr*(*s*), Fig. 17D]. In the type of *Cynognathus crateronotus* (BMNH R.2571) however, the origin of the scapular triceps is marked by a rugose tuberosity (see Seeley, 1895b: fig. 10).

The teres major, as reconstructed by Gregory and Camp (1918: 471) and Romer (1922b: Pl. XXXIII) in *Cynognathus*, takes origin from the caudal angle of the scapula. In all cynodonts the bone of the caudal (and cranial) angle is thicker than elsewhere on the scapular blade. In *Cynognathus* and *Diademodon* a groove on the thickened caudal edge below the angle is undoubtedly associated with the origin of the teres major (*t mj*, Figs. 17D, 19F). The medial wall of this groove extends posteriorly and serves as the origin for the serratus anterior musculature (Fig. 19F). A groove is not present in *Thrinaxodon* but the bone of the caudal angle is thickened; a

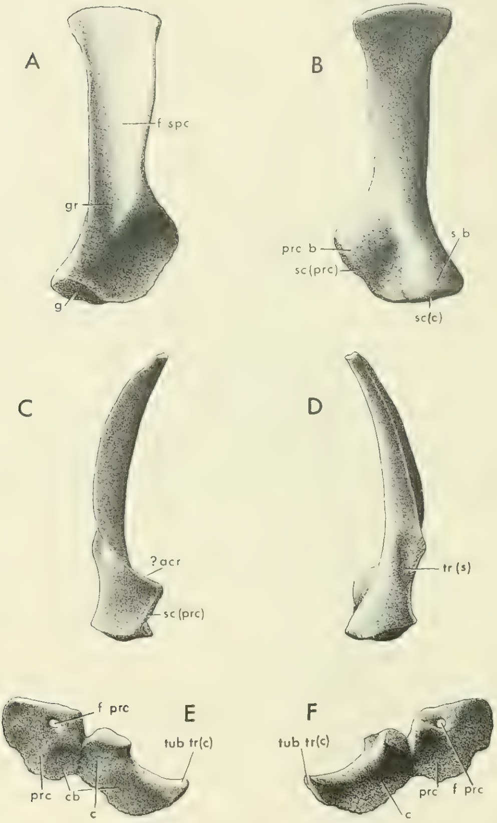

A
f spc
gr
g
B
s b
prc b
sc(prc)
sc(c)
C
?acr
sc (prc)
D
tr (s)
f prc
E
tub tr(c)
prc
cb
c
F
tub tr(c)
prc
f prc
c

FIG. 18. The scapulocoracoid of *Thrinaxodon*, SAM K. 1395. A, lateral; B, medial; C, anterior; D, posterior views of a right scapula. E, lateral; F, medial views of left procoracoid-coracoid plate which is incomplete along the ventral margin. X1.75. Abbreviations as in FIG. 17 except: *sc* (*c*), scapular articular surface for the coracoid; *sc* (*prc*), scapular articular surface for the procoracoid.

groove may have been developed on the unossified suprascapula which in large cynodonts permitted a dorsal extension of the groove.

With the exception of the muscle scars for the teres major and triceps the medial surface of the scapula is a smoothly curving, featureless plate which is readily described morphologically but which is difficult to interpret in terms of subscapular musculature. In medial view the scapular blade is concave dorsoventrally, except for a small area ventral to the vertebral border which is usually flat but which may be very shallowly concave (Figs. 17B, 18B). Anteroposteriorly the blade is convex, again with the exception of the area below the vertebral border.

The medial surface of the scapular blade may be roughly divided into cranial and caudal parts along the line of sharpest anteroposterior curvature. This line passes obliquely down the blade from the cranial angle posteroventrally to the joint between the supraglenoid buttress (*s b*) and the coracoid (*c*, Fig. 17B). The caudal part posterior to this line may be interpreted as the locus of origin of the Mm. subcoracoscapularis, serrati and levator scapulae (*sbcsc*, *ser* and *lev scap*, Fig. 20F); the cranial part represents the origin of the deltoid homologue, the dorsoscapularis (along the cranial border; *dsc*, Fig. 19F), and the insertion of part of the trapezius and levator scapulae musculature (*tzs*, *lev scap*, Fig. 20F).

Evidence for a reconstruction of cynodont subscapular musculature is derived from subscapular musculature in living reptiles and the inferred arrangement in other fossil forms. In *Sphenodon* and lizards the entire subscapular muscle mass, commonly referred to as the M. subcoracoscapularis, runs from an origin on the medial surface of the scapula and coracoid to the proximal internal angle of the humerus (*sbcsc*, Fig. 20D, E). This muscle is incompletely divided into posterodorsal and anteroventral divisions by a sterno-scapular ligament. The dorsal part is thought to be homologous with the M. subscapularis of mammals and in addition has fibers not represented in mammals which gain access to the lateral face of the scapula as the M. scapulohumeralis posterior (Romer, 1922b: 530–532; *sch p*, Fig. 19D, E). Anteroventral to the sterno-scapular ligament is the M. subcoracoideus; the question of its presence in cynodonts is discussed later with reference to the coracoid. Romer (1922b: 530) concluded that in primitive reptiles and pelycosaurs the entire subcoracoscapularis was confined to the dorsal half of the medial scapular blade and was probably not differentiated as in living reptiles. The origin is clearly defined as a shallow, triangular concavity, its "base" lying along the vertebral border and its "apex" pointing posteroventrally toward the glenoid (Fig. 20B, C). From the "apex" the subcoracoscapularis muscle passed posterolaterally around the caudal border of the scapula, where a broad trough is developed to facilitate its passage. The caudal part of the medial scapular surface in cynodonts is not greatly changed from this condition (Fig. 20F). The most significant differences are that the subcoracoscapularis origin extends nearly to the base of the scapula, as in mammals, and that the inserting end of the muscle does not circumvent the caudal border of blade as it did primitively, and still commonly does in living reptiles. Instead in cynodonts the insertion into the lesser tuberosity probably was reached by subcoraco-scapularis fibers emerging from the medial side of the scapula along the posterodorsal edge of the glenoid. This condition approximates that of mammals in which subscapularis fibers pass ventrally along the medial side of the glenoid capsule to reach the lesser tuberosity.

The cranial part of the medial scapular surface is a broad flange which faces primarily anteriorly and attenuates dorsally and ventrally (Figs. 17C, 18C). The cranial border in fact extends farther laterally than does the caudal border. It is improbable that the breadth of the cranial sector is in response to the requirements of the M. supracoracoideus alone (on the lateral face), but in view of the lack of muscle scars on this part of the medial surface it is impossible to reconstruct confidently the muscular arrangement. Levator scapulae and serratus musculature undoubtedly took origin from the area below the vertebral border (*lev scap*, *ser*, Fig. 20F), characterized in cynodonts by a lack of curvature in the blade and in some cases by a slight depression on the medial surface. Such a position is analogous to the origins of these muscles in living tetrapods as well as the inferred conditions in other fossil forms. The cranial section of the medial surface probably afforded insertional area for deep layers of the levator scapulae and possibly trapezius as well. Gregory and Camp (1918: Pl. XL) gave a reconstruction of the musculature on the medial side of the scapula of *Cynognathus*; this reconstruction, which delineates discrete areas for trapezius, omotrachelian and levator scapulae profundus musculature, is based primarily on an assumed analogy with *Ornithorhynchus*. However the medial side of the monotreme scapula is quite flat, as opposed to that in cynodonts which has a complex curvature. Furthermore the caudal half of the scapula is both shaped and oriented differently in monotremes. This difference is due in part to the posterior displacement of the caudal angle from which the teres major takes origin (a specialization common in fossorial forms); another peculiarity is the extensive invasion of the subscapularis (*sbsc*, Fig. 19G) onto the lateral surface (a development paralleled among reptiles; *sbcsc*, Fig. 19D, E). Neither of these features can be attributed to cynodonts. Monotremes offer no certain guide to the arrangement of cynodont subscapular musculature.

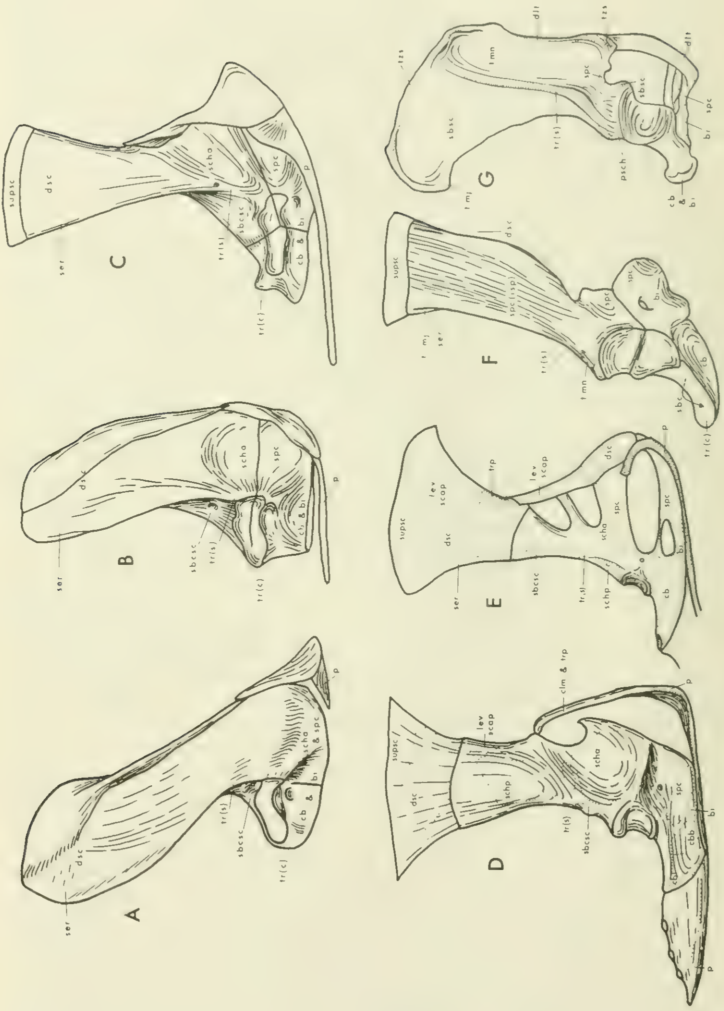
The base of the cynodont scapula bears a hemicircular articular facet, which is the scapular (dorsal) half of the glenoid (*g*, Fig. 18A), and two surfaces for articulation with the coracoids [*sc*(*prc*), *sc*(*c*), Fig. 18B, C]. The rough texture of all three bone surfaces testifies to an extensive cartilaginous covering during life. In old individuals the joint between the scapula and coracoids may synostose (Fig. 17), but in most specimens the cartilaginous connection resulted in postmortem disarticulation.

The scapular contact with the coracoids is buttressed by two rod-like processes, one for each coracoid, on the medial aspect of the scapular base (*s b*, *prc b*, Figs. 17B, 18B). The posterior or supraglenoid buttress, the larger of the two, is incompletely separated from the anterior or procoracoid buttress by a sulcus which leads into the procoracoid foramen below. This sulcus probably accommodated the nerve on its course to the foramen. The sutural surface of the anterior buttress is narrow, flat, and faces anteroventrally and somewhat medially [*sc*(*prc*), Fig. 18C]. It contacts a similar surface along the dorsal margin of the procoracoid. The sutural surface of the posterior buttress is slightly convex and wider than that of the anterior buttress. The separation between the surface on the posterior buttress for the procoracoid and the glenoid surface is marked by a difference in orientation, but the change is gradual.

The scapular surface of the glenoid faces posterolaterally as well as ventrally. The upper lip of the glenoid is sharply defined and the glenoidal surface below it is very slightly convex (Fig. 21). Otherwise the scapular half of the glenoid is rather flat; commonly there is a broad, shallow concavity situated at the facet center and the anterolateral corner of the facet faces laterally (Fig. 21). The margin of the coracoid (or lower) half of the glenoid is not as symmetrical in outline as the upper half. Compared with the hemicircular plan of the scapular half, the outline of the coracoid half of the glenoid is approximately triangular. The surface faces posterolaterally and slightly dorsally. Laterally the facet margin is gently convex and long; posteromedially the facet margin is straight and short, being terminated by a slight tuberosity (*tub*, Fig. 21) before reaching the scapular-coracoid contact. The facet surface is broadly convex, flattens gradually to an even slope near the lateral margin, and bears a distinct recess (*rec*, Fig. 21) adjacent to the posteromedial margin. Seeley (1895b: 91), Watson (1917a: 25) and Brink (1955: 29) claimed that the procoracoid was excluded from the glenoid but in fact its posterodorsal corner forms a small segment of the lateral glenoidal lip between the coracoid and scapula.

The coracoid and procoracoid are invariably synostosed along a serrate suture which is usually more clearly preserved on the medial side (Figs. 17B, 18E, 22A, B). The coracoid is approximately triangular in outline. The expanded, robust anterodorsal edge [*c*(*sc*), Fig. 22A] contacts the supraglenoid buttress above and acts to reinforce the coracoid part of the glenoid. The posterodorsal edge of the coracoid is a flat, wide shelf; the ventral edge is narrow and slightly convex. Both edges terminate posteriorly in a swollen tuberosity for the coracoid head of the triceps [*tub tr*(*c*), Figs. 17A, B, D, 18E, F, 22]. Romer (1922b: 538) believed that this head was absent in therapsids because of the "reduced condition" of the coracoid; however his figure (Pl. XXXIII) of *Cynognathus* appears to be based on the type of *C. crateronotus* Seeley 1895 (BMNH R.2571) in which the posterior half of the coracoid is broken off. Gregory and Camp (1918: Pl. XL) and McKenna (1961: fig. 6) also figured the same specimen; the former authors placed the origins of the coracobrachialis and biceps on the broken edge of the coracoid, giving no indication of the probable disposition of the triceps' coracoid head. Broom (1909: 284), comparing the type of *Cynognathus* with another "imperfect" specimen, also concluded that the coracoid was "singularly short, and not more than 10 mm. is missing . . . in the type specimen." In fact the cynodont coracoid has a long posterior process, a primitive feature which monotremes retain. However in monotremes (see Westling, 1889 and Howell, 1937a) the coracobrachialis and a biceps head attach to the coracoid process; the possibility that this was also the condition in cynodonts is discussed below (see p. 154).

The lateral margin of the dorsal coracoid shelf is sharply delineated by the undercut surface of the coracoid. The medial margin is a gradual transition from the dorsal shelf to the medial surface, especially adjacent to the coracoid tuberosity where the surfaces are smoothly confluent. In the living animal the dorsal shelf is interpreted as facing dorsolaterally, thus permitting a muscle originating from the medial surface to pass laterally to an insertion on the lesser tuberosity of the humerus. The relations of the M. subcoracoideus in *Sphenodon* and lizards (Fig. 20D, E) are analogous to this inferred condition in the cynodonts and it seems reasonable to believe, contrary to Romer (1922b: 531–532), that cynodonts possessed subcoracoid musculature. Romer rejected the possibility that *Cynognathus* possessed an M. subcoracoideus because there is "no evidence of a separation of the subcoraco-scapularis into two parts" (ibid.). This interpretation is based on the apparently "reduced" condition of the coracoid, which, as figured by Romer, is incomplete, and Romer's contention that the muscle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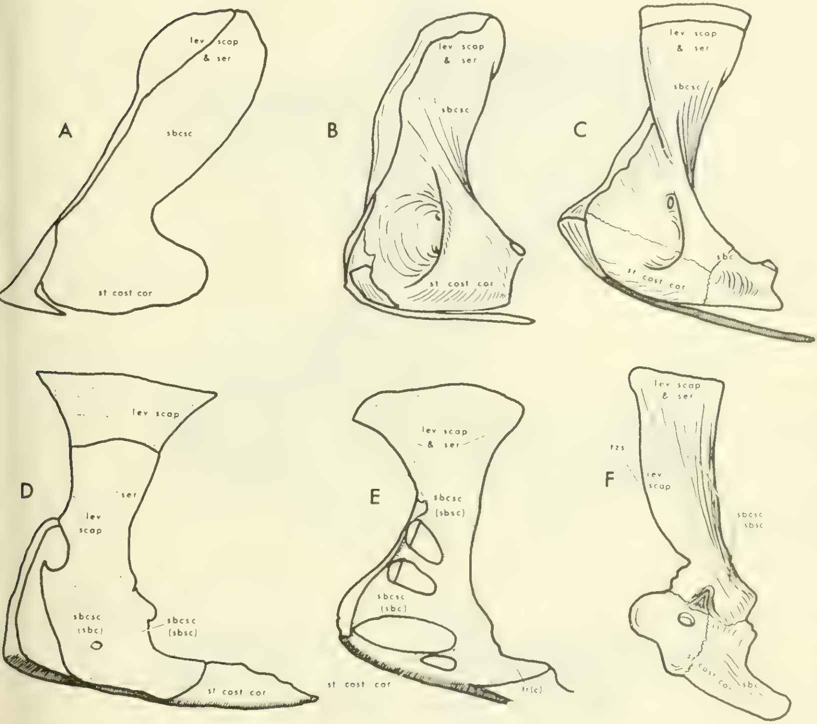
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FIG. 20. Diagrammatic medial view of the shoulder girdles of various tetrapods with actual (dotted lines) or reconstructed attachments of some major muscles. A, *Eryops*; B, *Diadectes*; C, *Dimetrodon*, modified after Romer, 1922b: Pl. 34; D, *Sphenodon*, after Furbringer, 1900; E, *Iguana*, after Romer, 1922b: Pl. 34; F, *Cynognathus*, clavicle and interclavicle not illustrated. Abbreviations: *st cost cor*, sterno-costo-coracoideus. For other abbreviations, see FIG. 19.

FIG. 19 (*left*). Diagrammatic lateral view of the shoulder girdles of various tetrapods with actual (dotted lines) or reconstructed attachments of some major muscles. A, *Eryops;* B, *Diadectes;* C, *Dimetrodon,* all after Romer, 1922b: Pl. 33; D, *Sphenodon,* modified after Furbringer, 1900; E, *Iguana,* after Romer, 1922b: Pl. 33; F, *Cynognathus,* clavicle and interclavicle not illustrated; G, *Tachyglossus,* after Westling, 1889: Pl. 2, and Howell, 1937a. Not to scale. Abbreviations: *bi,* biceps; *cb,* coracobrachialis; *cbb,* short head of coracobrachialis; *cbl,* long head of coracobrachialis; *clm,* cleidomastoideus; *dlt,* deltoid; *dsc,* dorsoscapularis; *isp,* infraspinatus; *lev scap,* levator scapulae; *p,* pectoralis; *psch,* proscapulohumeralis (see Howell, 1937a); *sbc,* subcoracoideus; *sbcsc,* subcoracoscapularis; *sbsc,* subscapularis; *scha,* scapulohumeralis anterior; *schp,* scapulohumeralis posterior; *ser,* serratus; *spc,* supracoracoideus; *supsc,* suprascapular cartilage; *t mj,* teres major; *t mn,* teres minor; *tr (c),* coracoid head of the triceps; *tr (s),* scapular head of the triceps; *trp,* trapezius; *tzs,* trapezius.

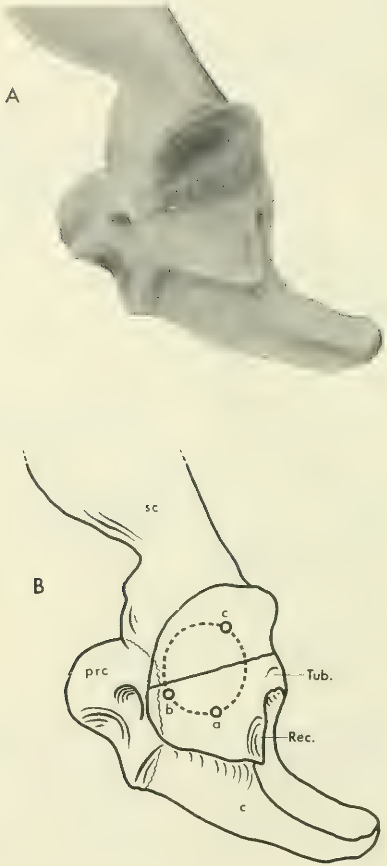

FIG. 21. A, sketch of the glenoid in a large cynodont, cf. ?*Cynognathus* (?*Diademodon*), NMB C.2711, in lateral view. B, in the line drawing of the same specimen, the dotted line represents the proposed course of a point on or near the center of the humeral head during locomotion: *a*, beginning of protractive phase; *b*, completion of protractive phase and beginning of propulsive movement; *c*, completion of propulsive movement. See text for details. Approx. X3/5. Abbreviations as in FIG. 17 except: *Rec*, recess; *Tub*, tubercle on coracoid half of the glenoid.

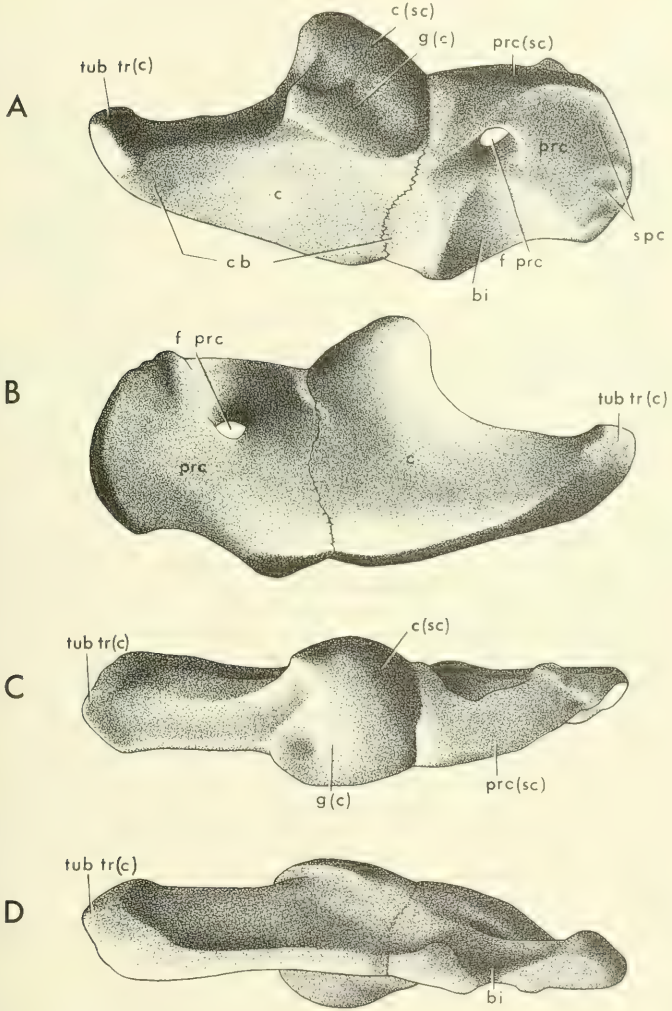
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FIG. 22. The right coracoid and procoracoid of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, in A, lateral; B, medial; C, dorsal; D, ventral views. X1. Abbreviations as in FIG. 17 except: *c* (*sc*), coracoid articular surface for the scapula; *g* (*c*), coracoid part of glenoid fossa; *prc* (*sc*), procoracoid articular surface for scapula; *spc*, fossa for supracoracoideus muscle.

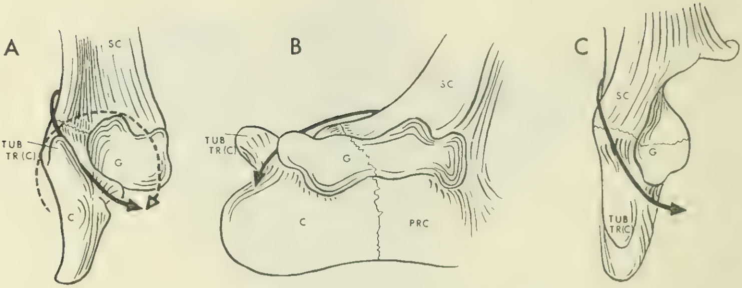

FIG. 23. Diagrammatic sketch of the glenoid region of *Dimetrodon* to show the probable course of the subcoracoideus muscle (black arrow). A, posterior; B, lateral; C, dorsal views. Romer (1922b) rejected Watson's (1917a) reconstruction of subcoracoid musculature (dotted line) on the basis that it would turn too great an angle (270°). Abbreviations as in Fig. 17.

was also absent in pelycosaurs. Romer correctly considered that a subcoracoideus origin from a fossa on the medial coracoid-procoracoid surface as proposed by Watson (1917a: 12) would require the fibers to turn an angle of approximately 270° (*dashed line*, Fig. 23A). Watson's reconstruction therefore seems improbable, but the possibility of a subcoracoideus cannot be eliminated on that account alone and the following alternative is proposed. In *Dimetrodon* as well as in most pelycosaurs, there is a distinct, broad groove in the dorsal rim of the scapulocoracoid between the tuberosity for the triceps' coracoid head and the posterodorsal rim of the glenoid (Figs. 23, 38; also see Romer and Price, 1940: 121–123). Medial to the dorsal rim of the glenoid, the sutural contact between the scapula and coracoid is swollen (Fig. 23C). This swollen rim creates a more gradual transitional surface from lateral to medial side than would be permitted by a narrower edge. Subcoracoid musculature, directed posterolaterally, could have taken origin from this swollen area as well as the adjoining medial surface; it could have reached the lesser tuberosity via the groove between the glenoid and the tuberosity for the coracoid head of the triceps without turning an angle of much more than 45°. The symmetrical and pulley-like shape of this groove is evidence of the passage of its tendon. Possibly the presence of a ligament over the groove served to restrict the course of the inserting end of the muscle. Thus reconstructed the M. subcoracoideus in pelycosaurs cannot have been a muscle of great power. The groove in cynodonts is widened to an elongate shelf, perhaps indicative of a relatively larger muscle.

In cynodonts the relationship between the tuberosity for the triceps' coracoid head and the glenoid is completely altered from the pelycosaurian condition. The tuberosity is displaced from its primitive location, posteromedial to the glenoid and at the same approximate level, to a position posteroventral to the glenoid and at a relatively much greater distance from it [*tr(c)*, Fig. 19C, F]. The modification as much represents a change in leverage for the triceps as it does an increase in the subcoracoid musculature which passed over the expanded shelf separating glenoid and tuberosity. Furthermore there is a change in the shape and orientation of the roughened surface area which gave rise to the triceps tendon. In pelycosaurs it is a convex, narrow strip capping the tuberosity, whereas in cynodonts it is a broad convexity, somewhat triangular in outline and facing posteroventrally. The functional significance of these changes will be discussed in a later section.

The lateral surface of the coracoid is indented to form a shallow fossa for the M. coracobrachialis origin (*cb*, Figs. 18E, 19F, 22A). The fossa extends onto the posteroventral corner of the lateral surface of the procoracoid. In some specimens (Figs. 18E, 22A) the fossa is vertically divided into anterior and posterior halves by a faint convexity. Such a division suggests differentiation of the muscle into a long (posterior) and a short (anterior) head as is common in lizards and *Sphenodon* (Furbringer, 1900).

The ventral margin of the coracoid (Fig. 22D) is a narrow continuation of the rugose surface on the tuberosity for the coracoid triceps. As a rounded edge which continues unchanged across the coracoid-procoracoid suture, its surface lacks laminar bone and its rugose texture is indicative of a cartilaginous extension.

The oval procoracoid is perforated, slightly posterodorsal of center, by a large procoracoid (or supracoracoid) foramen for the transmission of the N. supracoracoideus and blood vessels (*f prc*, Figs. 17, 18, 22). The foramen is sculptured to facilitate passage from a dorsomedial to a ventrolateral direction. The procoracoid plate is thickest at its posterodorsal corner where scapula, coracoid and procoracoid join to form the glenoid. Anterior to this point the width of the sutural contact between scapula and coracoid diminishes. On the lateral surface below the porcoracoid foramen is a hemicircular fossa, open ventrally, representing the origin of the M. biceps (*bi*, Figs. 19F, 22A). A ventrally directed ridge separates this fossa from that of coracobrachialis origin; a more anterior ridge, directed anteroventrally, separates the biceps origin from the remaining lateral surface of the procoracoid from which part of the supracoracoideus arises (*spc*, Figs. 19F, 22A). The ventral margin of the biceps fossa is a sharp, slightly concave keel (Fig. 22D); it connects the rugose and swollen terminal tuberosities of the ridges bordering the fossa, but shows no textural indication of having had a cartilaginous extension. The cranial margin of the procoracoid, between the terminal tuberosity of the anterior ridge and the procoracoid-scapular suture, is reflected laterally to create a very shallow fossa for supracoracoid musculature (Figs. 19F, 22A). The medial surface of the reflected margin (Fig. 22B) is beveled and bears the textured surface typical of cartilaginous overgrowth.

The medial aspect of the coracoid-procoracoid plate (Fig. 22B) is a rather flat surface devoid of prominent features. A shallow fossa below the glenoid buttress of the coracoid is probably associated with the insertion of sterno-costo-coracoid musculature (Fig. 20F). This fossa extends anteriorly for a short distance onto the procoracoid.

CLAVICLE (Fig. 24)

MATERIAL. Clavicles are adequately known in *Thrinaxodon* (AMMM 5265, SAM K.1395, USNM 22812) and from a collection of disarticulated skeletons of

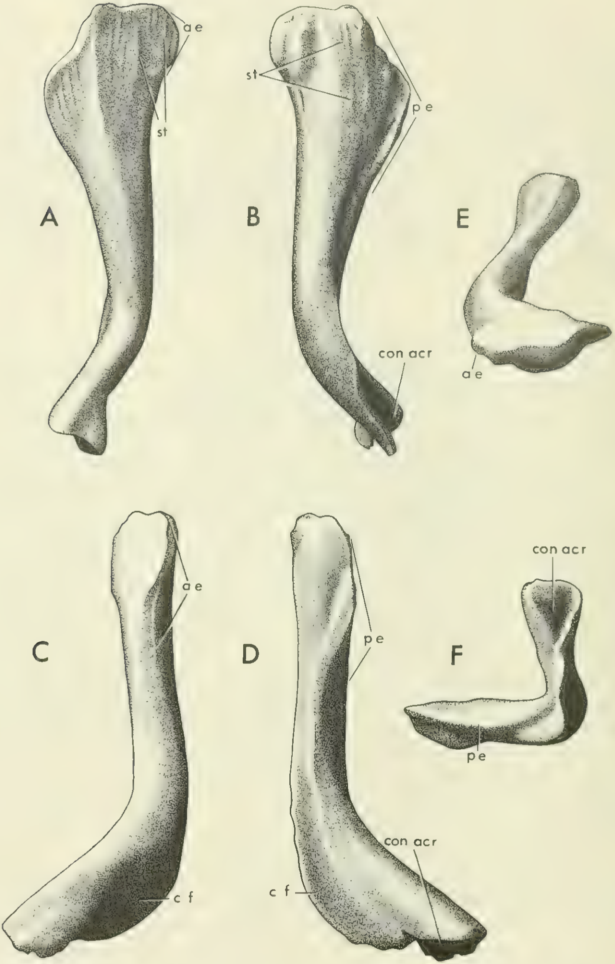

FIG. 24. Right clavicle of cf. ?*Cynognathus* (?*Diademodon*), NMB C.2700. A, dorsal; B, ventral; C, anterior; D, posterior views, with the medial and toward the top of the page. E, medial; F, lateral views. X2/3. Abbreviations: *a e,* anterior edge of medial end of clavicle, possibly the origin of cleido-mastoid musculature; *c f,* clavicular flange; *con acr,* concavity for reception of the acromial process; *p e,* posterior edge of medial half of clavicle; *st,* striations indicating ligamentous or other connective tissue binding clavicle to interclavicle.

Cynognathus and *Diademodon* (NMB C. 2700). Clavicles associated with an interclavicle are known in *Cynognathus* (Broom, 1909) and in a generically indeterminate cynognathid (Watson, 1917a: 24).

MORPHOLOGY. Disregarding minor differences in ossification, cynodont clavicles are morphologically alike and moderately robust. In dorsal view (Fig. 24A) the lateral third of the clavicle is a slender rod directed posterodorsally as well as laterally; the medial two-thirds consists of a gradually expanding, spatulate plate directed medially and horizontally. The long axes of the medial two-thirds and lateral third intersect at an angle of about 145°.

The clavicular facet for the acromion is a concavity formed on the slightly swollen lateral end of the clavicle (*con acr*, Fig. 24B, D, F). The depth of the concavity is accentuated by its thin, protracted edge which is invariably incompletely preserved and may have been continued as a ligament. This edge begins along the posterior aspect of the concavity, runs anterodorsally and then ventrally, thus encircling the top of the concavity but not the bottom. The edge is continued ventrally as a broad flange (*c f*, Fig. 24C, D) that imparts a considerable depth to the lateral third of the bone and probably functioned in the attachment of the clavicular deltoid.

The medial two-thirds of the clavicle is an expanded plate, thickest along its longitudinal axis. Numerous striations (*st*, Fig. 24A, B) parallel to this axis are incised on the dorsal surface and, to a lesser extent, on the ventral surface of the plate. These markings indicate ligamentous or other connective tissue joining the clavicle and interclavicle. The plate is bordered by rather sharply defined edges. The posterior edge of the plate in *Cynognathus* and *Diademodon* gradually arises close to the angle formed between the lateral third and medial two-thirds (*p e*, Fig. 24D) and is longer than the anterior edge (*a e*, Fig. 24C). The anterior edge is differentiated from the cylindrical clavicular shaft more abruptly, arising only near the medial end of the clavicle. To its edge, which is thicker than the posterior edge, may have attached cleidomastoid musculature. In *Thrinaxodon* the posterior edge of the plate is distinct from the clavicular shaft at about the midpoint of the clavicular shaft and therefore is shorter than in larger cynodonts. This gives the medial plate a more symmetrical, spoon-shaped appearance and is the only substantial difference between known cynodont clavicles.

INTERCLAVICLE (Fig. 25)

MATERIAL. The interclavicle is the least well-known element of the cynodont shoulder girdle. Only from *Thrinaxodon* (USNM 22812, Fig. 25A) has the interclavicle been recovered in sufficiently complete condition to permit full description. An isolated anterior fragment of an interclavicle (DMSW R.435), apparently but not certainly from a large cynodont, is available for comparison (Fig. 25B).

Broom (1909: 284) described an interclavicle of *Cynognathus* cf. *crateronotus*, but this specimen was not figured and is apparently lost. Watson (1917a: 25, fig. 9) described and figured an incomplete cynognathid interclavicle associated with a medial

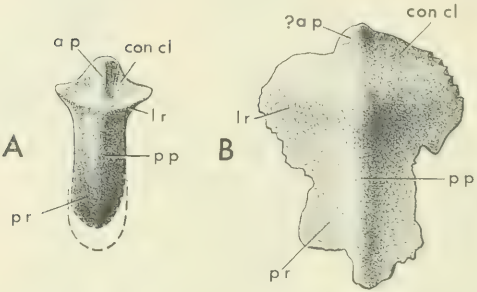

FIG. 25. Incomplete interclavicles of A, *Thrinaxodon* sp., USNM 22812, and B, an unidentified cynodont, DMSW R. 435. Ventral views. X1. Abbreviations: *a p*, anterior ridge, possibly for origin of part of pectoralis musculature; *con cl*, concavity for articulation with medial end of clavicle; *l r*, lateral ridge, delineating posterior border of concavity which receives the medial end of the clavicle; *p p*, posterior ridge, probable site of origin for the part of pectoralis musculature; *p r*, posterior ramus.

end of a clavicle. The specimen is possibly DMSW R.435, described below. The interclavicle of *Leavachia duvenhagei* (RC 92), originally described by Broom (1948: 623, fig. 40), is morphologically very similar to that in *Thrinaxodon*, although proportionately somewhat wider.

MORPHOLOGY. The interclavicle of *Thrinaxodon* is cruciate with a long posterior ramus. In ventral view (Fig. 25A) the anterior half bears a median tuberosity from which radiate four ridges; on either side two ridges pass anterolaterally (*l r*), while the remaining two pass directly anteriorly (*a p*) and posteriorly (*p p*), respectively. The anterior and lateral ridges define bilateral, triangular concavities for reception of the medial ends of the clavicles (*con cl*, Fig. 25A). The floor of these concavities is striated, just as are the medial clavicular extremities, indicating the presence of cartilage or perhaps ligamentous connective tissue. The anterior ridge (*a p*) separating the two concavities is a thin lamina of bone with vertical sides. The posterior ridge (*p p*), probably the site of origin for pectoral musculature, is most prominent anteriorly and gradually attenuates posteriorly. The posterior margin of this specimen is missing and was apparently very thin, but gives the impression that it widened transversely to a spoon-shaped terminus. Broom (1909: 284) noted a distinct widening of the posterior part of the interclavicle in *Cynognathus*, as did Watson (1917a: 25) for another cynodont interclavicle.

On the interclavicular fragment of the unidentified cynodont (Fig. 25B) most of the above named features, insofar as they are not obscured by breakage, are repeated. Yet none of the original edges of this specimen are preserved so the extent of the ridges cannot be compared to those in *Thrinaxodon*. The anterior ridge appears to be proportionally not as prominent as in *Thrinaxodon*, but this may be an artifact of breakage. A tubercle at the anterior extremity of the bone may represent the posterior extremity of a typical galesaurid type of ridge (*?a p*, Fig. 25B).

The cruciate pattern of the cynodont interclavicle is a certain mark of pelycosaurian heritage. Except for the slightly greater width of the posterior ramus, the interclavicle of *Thrinaxodon* essentially duplicates the interclavicular morphology of *Dimetrodon* (see Romer and Price, 1940: 118). However not all cynodont interclavicles retain a primitive pattern. The interclavicle of the *Exaeretodon*, a South American transversodontid, is short and triangular in form and bears a deep, median keel (Bonaparte, 1963a). Its morphology is clearly a specialized feature peculiar to this cynodont genus. The position of the keel is suggestive of a homology with the anterior ridge of the interclavicle described above. If so, the traversodontid keel might represent ossification of a plate which in galesaurids and other cynodonts was a cartilaginous (ventral) extension of the anterior ridge. Such a ridge, whether osseous or cartilaginous, would serve as an extensive area of origin for a massive pectoralis complex. Certainly the deltopectoral crest of the *Exaeretodon* humerus is no more robust or extensive than in other cynodonts, which is indirect evidence that the muscular attachments were not substantially different in traversodontids. The absence of a large interclavicular keel in non-traversodontid cynodonts might be explained on the basis of its having been cartilaginous. Otherwise it is difficult to account for the sudden appearance of this feature in traversodontids whose postcranial skeleton, for the most part, is little modified from a typical cynodont pattern.

2. FORELIMB

Humerus (Figs. 26–28)

MATERIAL. Humeri are adequately known in *Thrinaxodon* (SAM K.1395, AMMM 5265, USNM 22812, BPI 376 and NMB specimens described by Brink, 1954), in *Galesaurus* (SAM K.1119) and in *Diademodon* and *Cynognathus* from two collections where disarticulated skeletons of these two genera are preserved together (BPI 1675, NMB C.2693). Except for differences in size and ossification, all humeri are morphologically similar. In the National Museum (Bloemfontein) collection of *Diademodon* and *Cynognathus* (NMB C.2693), 17 complete or nearly complete humeri range in size from 58 to 178 mm. No consistent morphological differences among these bones could be discerned by which two genera might be distinguished, yet abundant cranial fragments attest to the presence of both genera. The conclusion is inescapable that the humeri of *Diademodon* and *Cynognathus* are essentially identical, although it is possible that large samples might show consistent differences in size.

The humeri of *Cricodon metabolus* and *Scalenodon augustifrons* were described by Crompton (1955b: 626, 652) and are morphologically indistinguishable from other large cynodont humeri. Incomplete humeri, also from the Manda Formation, are described by von Huene (1950), but these dissociated specimens are generically indeterminate.

Other known cynodont humeri are either referable to one of the above genera or are too poorly preserved or prepared to make adequate comparisons. Owen (1876: 21, Pl. XIX) described and figured the humerus of *Cynochampsa laniarius* (BMNH S.A. 43), the genus questionably synonymized with *Diademodon* by Watson and Romer (1956: 65). The humerus could be either that of a gomphodont or a cynognathid.

Seeley (1895a: 27–31) described a large humerus associated with *Gomphognathus* sp. (=*Diademodon*, see Brink, 1955, and Watson and Romer, 1956: 65), but admitted that it is so similar to that of *Cynognathus* that it might belong to this genus.

Seeley (1895a: 44–45) also described the well-preserved humerus of *Microgomphodon eumerus* (BMNH R.3581), but Brink (1955: 31) correctly recognized that this specimen probably represents a juvenile *Diademodon*.

Parrington's (1934) description of the humerus of *Galesaurus* (UMC R.2722) in fact was based on material which cannot be positively assigned to this genus (see above, p. 62). The material is unquestionably galesaurid, however, and does not differ from the *Thrinaxodon* pattern except for a slightly larger size. The same statement can be made of all other limb and girdle elements associated with this specimen.

The humeri from a disarticulated skeleton of *Glochinodontoides gracilis* (TM 83), described by Haughton (1924), are poorly preserved and only incompletely prepared. No substantial morphological differences are evident with which to contrast these humeri with those of the larger cynognathids and gomphodonts or those of the smaller galesaurids. The apparent reduced thickness of the proximal end, when compared to that in *Cynognathus* or *Diademodon*, is due to the lack of ossification of the head which is typical of smaller cynodonts.

Broom (1948: 623–624, fig. 42) described and figured the humerus of the procynosuchid *Leavachia duvenhagei* (RC 92). From his description it would appear to differ from other cynodont humeri only in having a longer and more prominent ectepicondylar flange. However, Brink and Kitching (1953a: 313–314), who performed additional preparation on this specimen, mentioned several inaccuracies in Broom's description of other skeletal elements and therefore Broom's figures are suspect. Now that the material is better prepared, it is obvious that the distal end of the humerus is entirely comparable to that in other cynodonts. Furthermore Broom claimed that the humeral length is 80 mm and the distal end width is 29 mm, giving a smaller length-width ratio (.36) than is typical of cynodonts (about .50). Measurements taken from his illustration (fig. 52, natural size), however, give a length of 79.5 mm and a distal width of 44 mm, yielding a ratio of .55 which is more comparable to that of other cynodonts.

MORPHOLOGY. Cynodont humeri more closely resemble those of primitive tetrapods in general and pelycosaurs in particular than those of any therian. In broad aspect the cynodont and monotreme, especially echidna, humerus are similar, but proportionally the monotreme humerus is much wider. This and other differences in morphological detail are probably the result of the latter's fossorial specialization and make a detailed comparison between the two of dubious value as far as interpreting cynodonts is concerned.

Humeral lengths range from about 3 cm in *Thrinaxodon* to about 20 cm in *Cynognathus* sp. The maximum width between epicondyles is invariably about one-half the length of the bone; femora of South American cynodonts were apparently more variable with regard to this feature (*Exaeretodon*, 54%; *Chiniquodon*, 58%; *Massetognathus*, 40%. See Bonaparte, 1963a, Romer, 1969a, Jenkins, 1970a). Maximal proximal width measured from the lesser tuberosity to deltopectoral crest is consistently 40% of total length. In cynodonts the inferred insertions of the Mm. supracoracoideus and subcoracoscapularis are not marked by actual (greater and lesser) tuberosities as are their homologues in mammals, Mm. spinati and subscapularis, respectively. However it is convenient to use this nomenclature in reference to these loci of insertion. The cynodont "lesser tuberosity" is best illustrated in Figure 26D as a bulbous area (*l t*) on the proximal, actually proximomedial, aspect of the humerus.

The broad deltopectoral crest constitutes about half the width of the proximal end (*d c*, Figs. 26–28), and the flaring of the epicondyles account for the distal breadth (*ec*, *en*, Figs. 26–28). The distal half of the humerus, triangular in outline, is essentially planar. The proximal half of the humerus is composed of two planes, the deltopectoral crest and the adjacent shaft, which intersect along the board bicipital groove at an angle of approximately 135° (*bi gr*, Fig. 27A). The short shaft connecting the expanded proximal and distal ends is triangular in cross-section and is only about ten percent of the total humeral length. The long axes of the two ends are "twisted" about the humeral axis so that in proximal view (Figs. 27A, 28D) they intersect at a 40 to 50° angle. The symmetry of the humerus is further complicated by dorsal flexure of the proximal half of the shaft (Figs. 26C,D, 28E,F).

The humeral head in all known specimens of *Thrinaxodon* and *Galesaurus* is incomplete and rather flat due to the fact that its terminus was extensively cartilaginous (*h*, Fig. 28A,D). There is no reason to believe, however, that the structure was different from that of larger cynodonts in which the head is better ossified. As preserved in *Diademodon* and *Cynognathus*, the humeral head is a low convexity centered on the strap-shaped surface of the proximal end (*h*, Fig. 27A). On average the articular surface faces anteromedially and somewhat dorsally. A dorsolaterally reflected lip raises the articular facet above the dorsal surface of the shaft (*l h*, Fig. 26A,C). Ventrally the articular facet is terminated along a clearly defined edge by intersection with the bicipital groove (Fig. 26B). The anterior (or lateral) and posterior (or medial) limits of the head are not obvious in most specimens because the surfaces of the head and adjacent tuberosities are confluent along the narrow, strap-shaped surface of the proximal end. The roughened texture of this entire surface indicates a cartilaginous overgrowth. The insertion of the M. subcoracoscapularis (lesser tuberosity) is inferred to be medially adjacent to the head on the bulbous proximomedial corner of the humerus (*l t*, Fig. 26A,B,D). In several specimens (NMB C.2693) the lesser tuberosity appears to be set apart from the head by a slight depression cutting across the strap-shaped end surface on which both are situated (Fig. 27A). The insertion of the M. supracoracoideus (greater tuberosity) is inferred to be on the proximolateral corner of the humerus at the junction of the head and deltopectoral crest (*g t*, Fig. 26A-C). This corner, unlike the proximomedial corner, is broadly rounded and narrow. The rugose surface continues distally along the deltopectoral crest for almost one-third of its length.

The deltopectoral "crest" is a rather rectangular flange, thickest along its junction with the shaft (*d c*, Figs. 26-28). The relatively thick proximal third of its free margin

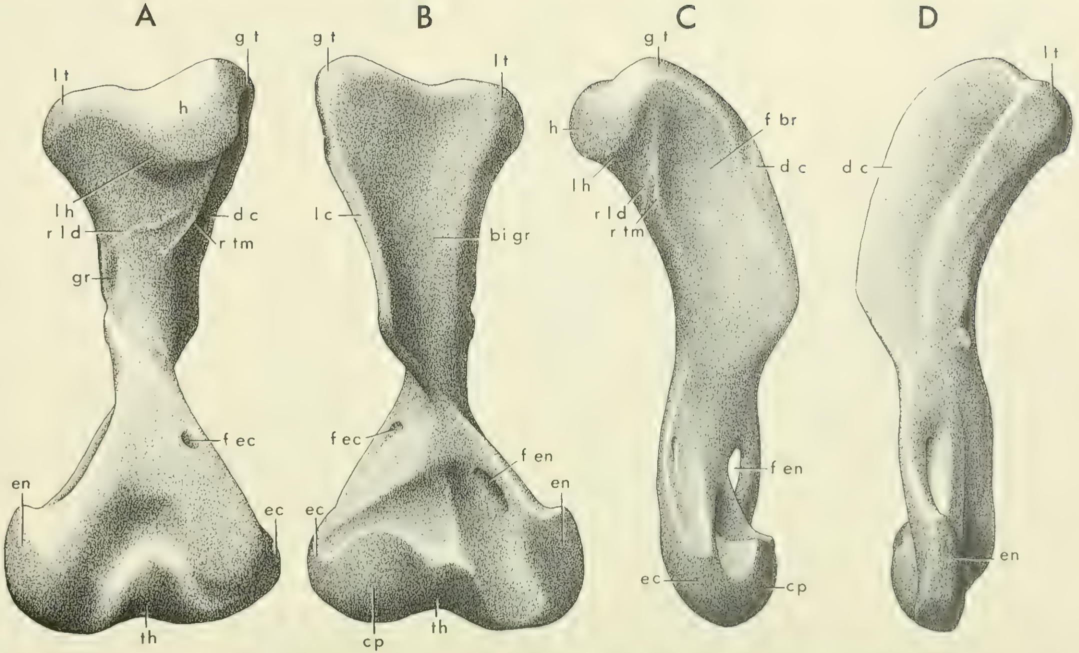
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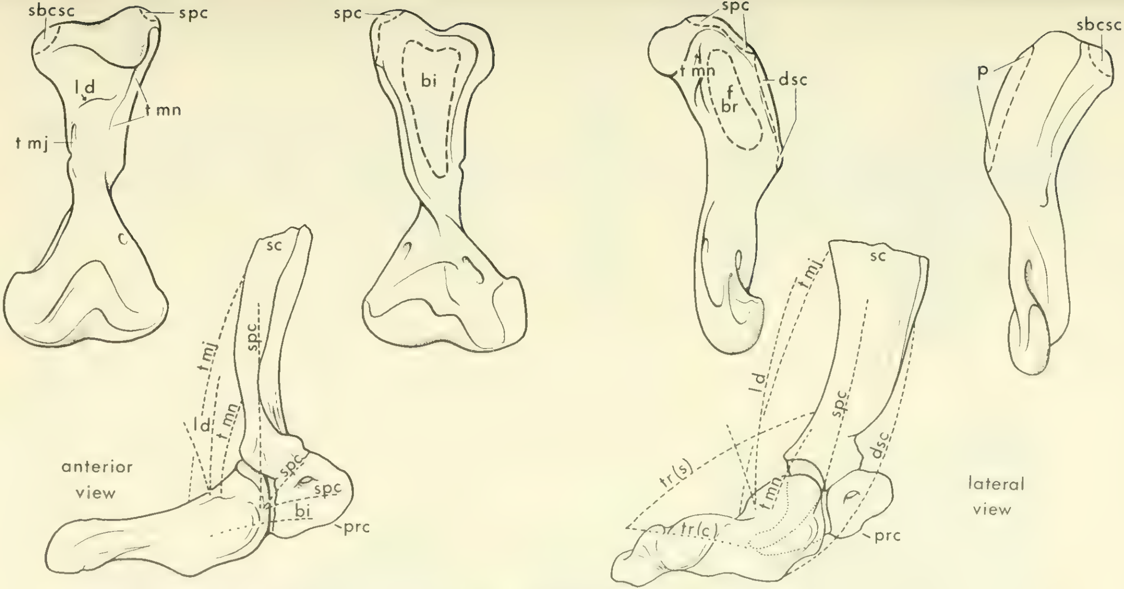
FIG. 26. Part I. Right humerus of cf. ?*Cynognathus* (?*Diademodon*), NMB C.2693, in A, dorsal; B, ventral; C, anterolateral; D, posteromedial views. X1.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l d
t mn
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spc
bi
prc
anterior
view
sc
t mj
l d
spc
dsc
tr(s)
t mn
tr(c)
prc
lateral
view

FIG. 26. Part II. The line drawing above gives reconstructed muscle insertions and, below, the presumed orientation of some of the shoulder muscles in anterior and lateral views. Abbreviations: *bi*, biceps; *bi gr*, bicipital groove; *cp*, capitulum; *d c*, deltopectoral crest; *dsc*, dorsoscapularis; *ec*, ectepicondyle; *en*, entepicondyle; *f br*, fossa probably related to brachialis origin; *f ec*, ectepicondylar foramen; *f en*, entepicondylar foramen; *g t*, greater tuberosity; *gr*, groove possibly representing the insertion of the teres major; *h*, humeral head; *l d*, latissimus dorsi; *l h*, dorsal lip of the humeral head; *l t*, lesser tuberosity; *p*, pectoralis musculature; *prc*, procoracoid; *r l d*, ridge possibly representing the insertion of the latissimus dorsi; *r tm*, ridge possibly representing the insertion of the teres minor; *sbcsc*, subcoracoscapularis; *sc*, scapula; *spc*, supracoracoideus; *th*, trochlea; *tr (c)*, coracoid head of triceps; *tr (s)*, scapular head of triceps; *t mj*; teres major; *t mn*, teres minor.

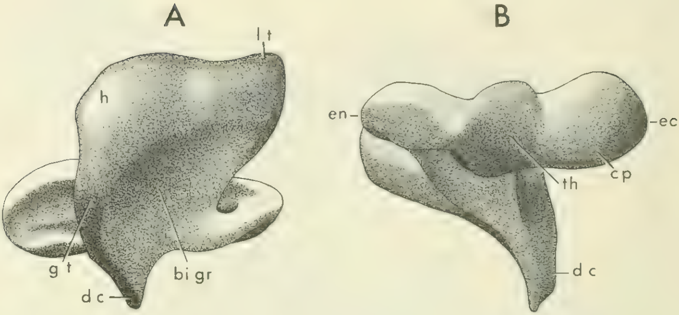

FIG. 27. A, proximal; B, distal views of humerus illustrated in FIG. 26. X1. Abbreviations as in FIG. 26.

was probably occupied by supracoracoid insertion. The remainder of the margin is beveled on both sides, creating a sharp edge bowed slightly ventrally (Fig. 26B,C). The flange abruptly terminates at a small marginal tuberosity equidistant from the proximal and distal ends of the humerus; from this tuberosity a low ridge runs posterodistally to bridge the entepicondylar foramen.

Deltoid musculature may be reconstructed as inserting on the beveled anterolateral margin and terminal tuberosity of the deltopectoral crest. The entire posteromedial margin of the crest margin bears a pattern of striations and rugosity which may indicate the M. pectoralis insertion. The entire anterolateral surface of the deltopectoral crest is occupied by a shallow but broad fossa (*f br*, Figs. 26C, 28E) probably representing the origin of the M. brachialis. A prominent ridge runs anteroproximally between the fossa and the humeral head (*r tm*, Fig. 26A) and may possibly indicate the insertion for a teres minor.

From the ridge just described another ridge runs obliquely across the dorsal surface of the humeral shaft (*r l d*, Fig. 26A). It is low and irregular and conceivably represents the insertion for the M. latissimus dorsi. A groove, more distally placed, parallels the shaft along its posteromedial aspect (*gr*, Fig. 26A). In one excellently preserved specimen (BPI 1675) it is clear that the irregular ridge and groove are confluent, and therefore the groove may represent the initial differentiation of the insertion of the M. teres major from that of the M. latissimus dorsi. It is equally possible that one or both of these features represents the origin of one of the humeral triceps heads.

Oval entepi- and ectepicondylar foramina pass distoventrally through the bone adjacent to the epicondyles and each is obliquely inclined away from the shaft. Broom (1948: 624) claimed than an ectepicondylar foramen is absent in *Thrinaxodon*, but it is clearly present in all known specimens except where lost through breakage. The ectepicondylar foramen (*f ec*, Figs. 26A, 28A) is at least half the size of the other and is enclosed by a thin flange with a slightly swollen margin. Romer (1922b: 538–539) suggested that the ectepicondylar foramen was formed during the course of distal

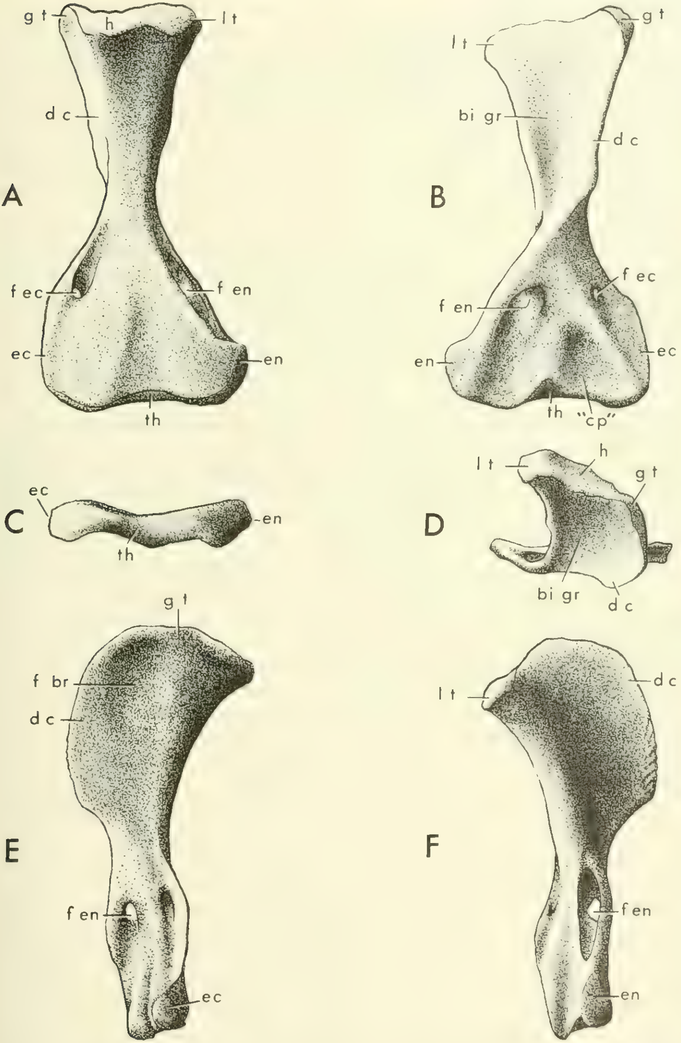
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FIG. 28. Left humerus of *Thrinaxodon*, SAM K. 1395, in A, dorsal; B, ventral; C, distal; D, proximal; E, anterolateral; F, posteromedial views. X2. Abbreviations as in FIG. 26 except: "*cp*", area of humeroradial articulation, with capitulum not preserved as a rounded eminence.

migration of supinator musculature. In most pelycosaurs the supinator tuberosity on the shaft and the ectepicondyle are separated by a groove through which passed a branch of the radial nerve. With further elongation of the shaft in later forms the musculature arising from the supinator tuberosity migrates distally with the extensor muscles and the radial nerve is enclosed by a bony flange which permits muscular origin in the region around the nerve. In most mammals the foramen is completely lost, but in *Didelphis* there often occurs a proximal groove in the supinator crest which represents the distal half of the "bypassed" foramen. In cynodonts the foramen is proximally placed and therefore closely approximates a mammalian condition.

The long, oval entepicondylar foramen is enclosed by a stout rod of bone which, as noted before, is the distal continuation of the deltopectoral flange. Romer (1922b: 557) suggested that its formation in primitive tetrapods resulted from the proximal expansion of flexor musculature. The median nerve became enclosed by the proximal extension of bone surface required for flexor origins. This foramen is lost in most mammals, but is retained in the more primitive forms such as *Didelphis* where its form and orientation are almost identical with that in cynodonts.

The entepicondyle is a stout process bearing a curved, strap-shaped terminal margin (*en*, Fig. 26D). The margin is rugose in texture, indicating cartilaginous extension, and extends from near the distal extremity of the entepicondylar foramen around to the trochlea (Fig. 27B). The entepicondyle is displaced farther from the radioulnar facet than is the ectepicondyle and as a result the triangular distal end of the humerus is somewhat asymmetrical. This condition parallels that in monotremes and increases the flexor leverage in the forearm.

In the larger cynodonts the ectepicondyle is a broad swelling on the distolateral corner of the humerus (*ec*, Fig. 26C). Its thickness, which is greater than that of the entepicondyle (*en*, Fig. 27B), possibly correlates with its position partially overlying the capitulum and the need for a strong buttress for weight transference to the radius. In smaller cynodonts such as *Thrinaxodon* in which weight was not such a critical factor, the ectepicondylar thickness is less than that of the entepicondyle (Fig. 28C). In no cynodont does the rugose terminal surface for forearm extensor musculature origin extend as far proximally as does the similar surface of the entepicondyle. However extensor origins may have continued proximally along the thin ectepicondylar flange (or ridge) which bridges the ectepicondylar foramen.

The trochlea in *Diademodon* and *Cynognathus* is a broad groove occupying about one-quarter of the total distal end width (*th*, Fig. 27B). It is extended onto the dorsal and ventral aspects of the humerus by lips raised above the respective surfaces (Fig. 26A,B); the ventral lip, somewhat wider than the dorsal, merges with the adjacent capitulum. From dorsal to ventral extremities the trochlea turns an angle of 180°. Its dorsoventral axis (seen in end view) is oblique to the long axis of the distal end, i.e., the dorsal lip is more anteriorly situated than the ventral (Fig. 27B). In *Thrinaxodon* and *Galesaurus* the trochlea is not well ossified (*th*, Fig. 26A-C), but in view of the other close similarities between cynodont humeri, it seems probable that the trochlea in these genera was essentially identical to that of larger forms.

The capitulum in *Diademodon* and *Cynognathus* is a board, low convexity occupying almost forty percent of the total distal end width (*cp*, Fig. 26B). The facet is entirely confined to the ventral aspect of the humerus where its rugose surface is confluent posteromedially with the trochlea and anterolaterally with the ectepicondyle. In *Thrinaxodon* and *Galesaurus* the capitulum is a round concavity in the same position ("*cp*", Fig. 28B). It appears probable that this is due to a lack of ossification of a bulbous facet which, as in larger forms, articulated with the slightly concave proximal facet of the radius.

RADIUS (Figs. 29, 30)

MATERIAL. Cynodont radii are known in *Thrinaxodon* (SAM K.1395), *Galesaurus* (SAM K.1119), and *Cynognathus* and *Diademodon* from two collections (BPI 1675, NMB C.2697) in which disarticulated skeletons of these two genera are preserved together. Broom (1948: 625) gave a diagrammatic figure and an inadequate description of the radius in *Leavachia duvenhagei* (RC 92); comparison of the procynosuchid radius with that of later cynodonts must await further study.

MORPHOLOGY. The cynodont radius (Figs. 29, 30) is a simple, cylindrical bone with expanded ends and in general aspect resembles a pelycosaur radius. The distal half of the shaft is curved slightly medially to facilitate passage of the radius over the anterodistal surface of the ulna. In larger cynodonts the proximal articular facet is hemicircular, with a straight edge along the posteromedial aspect. The facet surface is concave anteroposteriorly and slopes medially (*pr ar f*, Fig. 29C). In *Thrinaxodon* and *Galesaurus* the poorly ossified proximal end is an even, very shallow depression, but in outline and in orientation it resembles that of larger cynodonts (*pr ar f*, Fig. 30A,C).

In larger cynodonts a tuberosity occurs on the posteromedial aspect of the proximal end below the capitular facet (Fig. 29B). This tuberosity bears a facet (*f u*, Fig. 29A,B) for articulation with the radial notch of the ulna. In mammals the same facet forms a strap-shaped circumference around the radial head for 180° or more. The circumferential extent in cynodonts appears to have been on the order of 70°-90°, and the degree of pronation and supination possible must have been correspondingly less than in most mammals. The same tuberosity and facet in *Thrinaxodon* (*f u*, Fig. 30B) and *Galesaurus* is inconspicuous and would be overlooked if the better ossified radii of larger cynodonts were not available.

A ridge (*r*, Figs. 29B,C, 30B,C) from the anterior aspect of the ulnar facet passes down the posteromedial side of the shaft. It gradually attenuates and is lost near the middle of the shaft. In larger cynodonts the ridge bears a distinct swelling at about its midpoint which may represent a radial tuberosity for insertion of the biceps. Medial to this swelling is a fossa (*r f*, Fig. 29B,C) possibly also representing the insertion of a major antebrachial flexor. Two faint lineations, each representing a muscular or ligamentous "scar", run obliquely down the shaft from the swelling. The posterior (*pl*, Fig. 29B,D) is the longer of the two, traceable in larger cynodonts to nearly the distal end. Its position suggests that it is the origin of a flexor muscle. In *Galesaurus* (SAM K.1119) and in *Thrinaxodon* this feature is represented by a distinct crest (*pl*, Fig. 30D). The anterior lineation (*al*, Fig. 29C) rather closely parallels the anterior crest

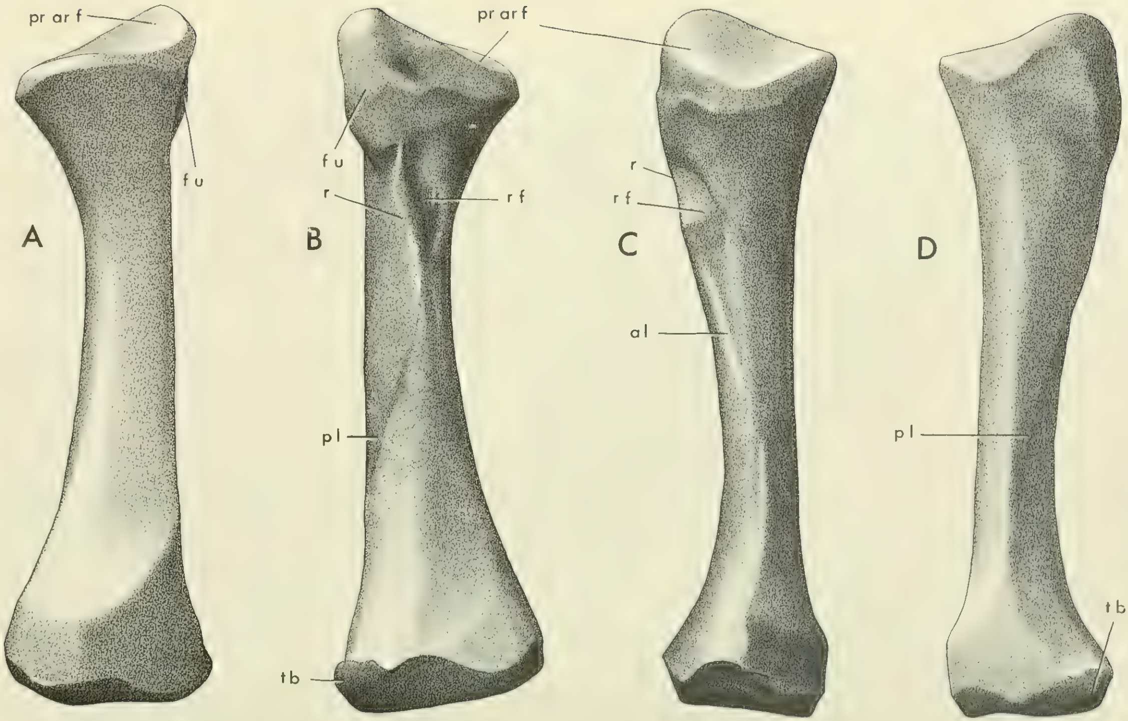


FIG. 29. Left radius of cf. ?*Cynognathus* (?*Diademodon*) BPI 1675 in A, anterior; B, posterior; C, medial; D, lateral views. X1. Abbreviations: *a l*, anterior lineation; *f u*, facet for articulation with radial notch of ulna; *p l*, posterior lineation; *pr ar f*, proximal articular facet; *r*, ridge bearing radial tuberosity; *r f*, fossa possibly representing the insertion of an antebrachial flexor; *tb*, tuberosity for ulnar contact.

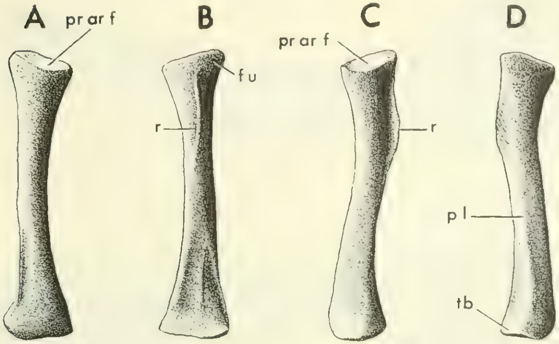


FIG. 30. Right radius of *Thrinaxodon*, SAM K. 1395, in A, anterior; B, posterior; C, medial; D, lateral views. X2. Abbreviations as in FIG. 29.

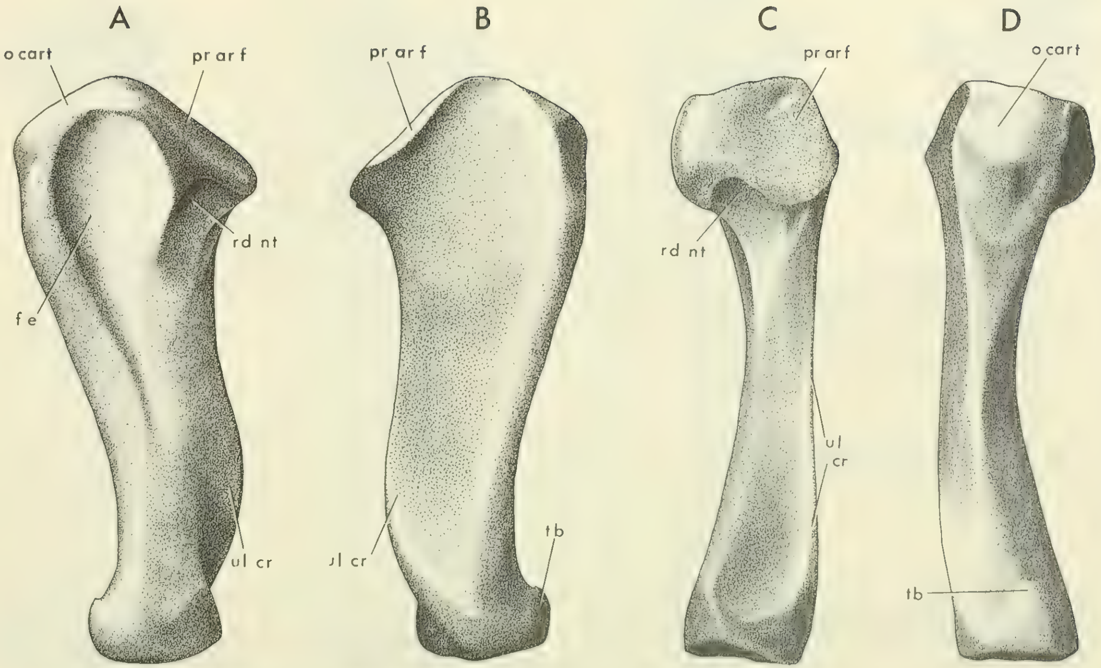
of the ulna from which a radio-ulnar interosseous ligament probably arose. This lineation perhaps represents the radial attachment of this ligament.

The distal end of the radius is triangular in outline. The articular facet is a shallow depression approximately equal in area to that of the proximal end. The rim of the facet was apparently cartilaginous and therefore is not preserved in any specimen. Along the posterolateral aspect of the rim is a tuberosity (*tb*, Fig. 29B,D) which apparently made contact with the anteromedial aspect of the distal end of the ulna.

ULNA (Figs. 31, 32)

MATERIAL. Cynodont ulnae are known in *Thrinaxodon* (AMMM 5265, SAM K. 1395, BPI 287, BPI 376), in *Galesaurus* (SAM K.1119), and in *Cynognathus* and *Diademodon* from two collections in which the disarticulated skeletons of these two genera are preserved together (BPI 1675, NMB C.2695). Broom's (1948: 624–625) description of the ulna in *Leavachia duvenhagei* (RC 92) was criticized by Brink and Kitching (1953a: 314) for inaccuracy but no specific corrections or redescription were given. Brink and Kitching's figure shows the ulna, although incompletely exposed, is apparently similar in morphology and proportion to those of other cynodonts.

MORPHOLOGY. The cynodont ulna is short and robust relative to typical mammalian ulnae. The only major difference between the ulnae of galesaurids and larger cynodonts is that the former are consistently more slender and gracile (cf. Figs. 31 and 32). In addition to this basic proportional difference galesaurid ulnae are not as well ossified as in larger cynodonts; a detailed comparison of features would reveal many apparent differences, but in fact most of these are the result of differences in degree of ossification.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C
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FIG. 31. Right ulna of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, in A, lateral; B, medial, C, anterior, D, posterior views. X3/4. *f e*, fossa presumably for an extensor muscle origin; *o cart*, osseous base from which a presumably cartilaginous olecranon process arose; *pr ar f*, proximal articular facet; *rd nt*, radial notch: *tb*, tubercle possibly representing the attachment of an extensor muscle; *ul cr*, ulnar crest.

In lateral view the sigmoidal shape resembles the outline of generalized mammalian ulnae, but a high crest (*ul cr*, Figs. 31A–C, 32A–C) along the anteromedial margin imparts a depth to the bone quite uncharacteristic of mammalian proportions. In anterior view (Figs. 31C, 32C) the shaft is very narrow, with the distal end evenly expanding mediolaterally and the proximal end expanding primarily laterally.

An ossified olecranon is absent. The proximal end of the ulna, homologous with the point where an olecranon develops in mammals, is very wide and the bone is cancellous (*o cart*, Figs. 31A,D, 32B,D). A broad, cartilaginous olecranon appears a probability on this evidence (see Fig. 42) but is virtually necessitated by previously cited evidence for well-developed triceps musculature, especially the coracoid head.

The cartilaginous olecranon probably contributed to the formation of a hemicircular semilunar notch. As preserved, however, the "notch" is merely a very slightly concave, oval facet (*pr ar f*, Fig. 31A–C) adjoining the surface from which the inferred olecranon arose. The facet as a whole is inclined anteriorly (relative to the shaft axis) at an angle of 45° but also slopes laterally to a small degree.

On the lateral surface of the proximal end are two fossae which are invariably well developed. The anterior and smaller of the two (*rd nt*, Fig. 31A), analogous to the "radial notch" of mammals, is limited to a triangular area immediately distolateral to the sigmoid facet and receives the tubercle on the proximal end of the radius. This fossa is poorly developed in galesaurids. The posterior fossa (*f e*, Figs. 31A, 32A) is a smooth, spoon-shaped depression which abruptly attenuates distally and terminates between the middle and distal thirds. In galesaurids it commonly does not extend so

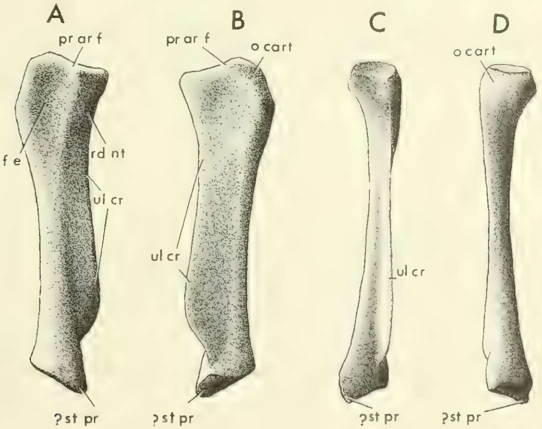


FIG. 32. Right ulna of *Thrinaxodon*, SAM K. 1395, in A, lateral; B, medial; C, anterior; D, posterior views. X1.7. Abbreviations as in FIG. 31 except: *? st pr*, styloid process questionably homologous with the styloid process found in mammals.

far distally. Its position and orientation is consonant with the interpretation that it served for the origin of an extensor muscle, possibly the M. extensor carpi ulnaris.

A high, narrow crest (*ul cr*, Figs. 31A–C, 32A–C), commencing at the anteromedial margin of the sigmoid notch, passes distally along the anteromedial aspect of the shaft. Proximally its slightly concave edge parallels the shaft axis; distally the convex edge curves medially to permit passage of the radius across the anteromedial aspect of the ulna. Haines (1946: 9) proposed that the crest (described in ?*Galesaurus* by Parrington, 1934: 60) served as the insertion for a radio-ulnar interosseous ligament. Haines' interpretation is valid although his observation that the crest was directed laterally is incorrect.

The medial surface of the ulna is smooth and almost featureless except for two confluent, shallow fossae (Fig. 31B) probably associated with the origin of deep flexor musculature. As with other features, these fossae are relatively less developed in galesaurids.

In larger cynodonts the distal articular facet is somewhat triangular in outline with a posterior "apex" and an anterior "base". The surface, bearing textural rugosity typical of the ends of cynodont limb bones, is anteroposteriorly convex. A line from the most posterior point on the surface, or "apex", to the anterolateral corner of the triangular facet follows a slight groove which describes a segment of a large circle. This line represents the anteroposterior axis of movement of the ulna on the ulnare. The distal end of galesaurid ulnae appears to be somewhat different, although in no known specimen is the end perfectly preserved. The articular area is more or less oval in outline and is set obliquely across the shaft. The anterior aspect of the facet is drawn to a blunt point (?*st pr*, Fig. 32), giving the appearance of a styloid process as in some mammalian ulnae. No trace of this feature is found in larger cynodonts.

The rim of the distal articular facet is invariably poorly preserved but in all larger specimens a tuberosity (*tb*, Fig. 31B,D) is preserved at the posterior corner ("apex") which possibly represents an insertion for a long extensor. This tuberosity is small and indistinct in galesaurids.

MANUS (Figs. 33, 34A, 35)

MATERIAL. The cynodont manus is inadequately known because of poor ossification in a small number of available specimens. Only two specimens, *Thrinaxodon liorhinus* (UMC R.2733; see Parrington 1933; 1939) and *Diademodon* sp. (USNM 23352), have an apparently complete set of carpal bones, but neither is in complete articulation and the latter is poorly preserved. An acid prepared manus of *Thrinaxodon* sp. (SAM K.1395) shows details of the proximal carpals not seen elsewhere, but only seven ossicles are preserved from the (presumably) original eleven. Most of the phalanges are present.

The apparently complete and articulated carpus of *Leavachia duvenhagei* (RC 92) described by Broom (1948: 624 625) lacks the second distal carpal (Brink and Kitching, 1953a: 314).

An incomplete carpus is known for *Galesaurus* (SAM K.1119).

The specimens of *Thrinaxodon* and *Diademodon* agree with Broom's (1932b:

264) observation that *Thrinaxodon* and "a large *Cynognathus*-like cynodont" have four elements in the proximal row; radiale, intermedium, ulnare, and pisiform.

CARPUS

MORPHOLOGY. The ulnare, known adequately from *Thrinaxodon* (*u*, Fig. 33) and *Galesaurus*, is the only cynodont carpal of which the orientation is certain. The galesaurid ulnare is stout, rectangular, and somewhat longer than wide, with a dorsal facet for the distal end of the ulna. The facet is saddle-shaped, the anterior and posterior halves rising only a small amount. Occupying the ventral surface is a round, shallow concavity. The dorsoventral thickness of the bone is greater medially than laterally so that in transverse cross-section the bone is triangular. The anterior face bears a flat, vertical facet for articulation with the fourth and possibly fifth (if present) distal carpal; the medial surface bears a deep groove for the reception of the intermedium. The ulnare in *Diademodon* (*u*, Fig. 34A) is transversely constricted and anteroposteriorly longer along its lateral edge than it is along its medial edge, thus differing from the rectangular shape in galesaurids. In *Leavachia* the ulnare as figured by Broom (1948: 625) is slightly constricted as in *Diademodon*, but the lateral and medial edges are subequal in length, imparting a rectangular outline as in galesaurids.

The intermedium in *Thrinaxodon* and *Galesaurus* is a flat, rectangular bone, of which one of the two longer edges is concave, the other convex. Damage and uncleared matrix on UMC R.2733 (Fig. 33) prohibits positive identification of the intermedium in this specimen, but this element is known from other specimens (SAM K.1395, SAM K.1119). The precise orientation of the intermedium is not known with certainty, but the following interpretation is most likely. The long axis is anteroposterior, with the two featureless, flat faces representing dorsal and ventral aspects. The concave (medial) long edge forms a strap-shaped facet which articulates with the rounded lateral surface of the radiale. The opposite (lateral) long edge is slightly convex and is received by a groove in the medial aspect of the ulnare. At the middle of the ventral edge of the ulnare groove is a swelling that is opposed by a slight depression on the anterolateral corner of the intermedium ventral surface. In *Diademodon* the articular relationships of the intermedium (*i*, Fig. 34A) with the radiale and ulnare are apparently the same as in galesaurids, although the bone is relatively narrower.

The radiale in *Thrinaxodon* (*r*, Fig. 33) and *Galesaurus* is a stout, oval nodule and is approximately one-third again as thick through its center than is the ulnare through its medial (thickest) edge. The dorsal surface of the radiale is a rounded facet for articulation with the radius. The medial and posterior faces of the radiale are nearly vertical. On the flat ventral surface there are two slight depressions separated by a low, oblique ridge, features which represent ligamentous or muscular attachment. The anterior face is incised with a wide, transverse groove for reception of the medial centrale. The radiale in *Diademodon* (*r*, Fig. 34A) is similar to that in galesaurids. The flat, ventral surface appears to differ in the presence of a broad groove opening onto the posterior margin and a tuberosity on the posterolateral corner. The radiale of *Leavachia* is "irregularly quadrangular" (Broom, 1948: 624), contrasting to the oval shape of later cynodonts.

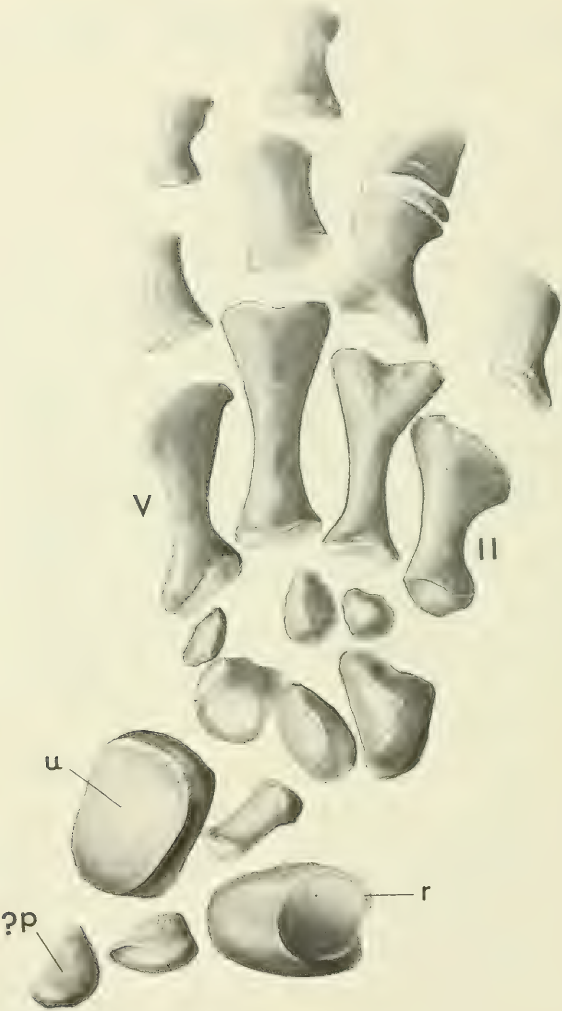


FIG. 33. Manus of *Thrinaxodon liorhinus*, UMC R. 2733, showing eleven carpals. Distal phalanges and first digit not illustrated in this view (see Parrington, 1939). Approx. X5.7. Abbreviations: *II-V*, metacarpals II-V; ?*p*, pisiform, identification uncertain; *r*, radiale; *u*, ulnare.

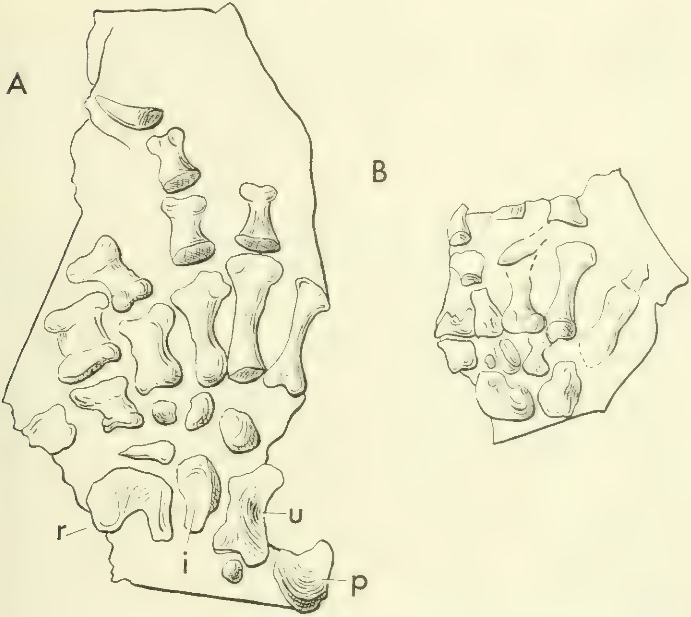


FIG. 34. A, manus and B, pes of *Diademodon* sp., USNM 23352, showing disparity in size X1.5. Abbreviations as in FIG. 33 except: *i*, intermedium.

A pisiform is known in *Thrinaxodon* (UMC R. 2733, in which the 11 carpals are disarticulated), in *Diademodon* (USNM 23352) and in *Leavachia* (RC 92). In *Thrinaxodon* the identity of the pisiform is somewhat in doubt, the probability being that it is one of the two elements preserved posterior to the ulnare (see Parrington, 1939: fig. 1). The more posterior of the two is closest to the proximolateral corner of the ulnare with which, in addition to the ulna, the pisiform typically articulates and is here considered to be the pisiform. The bone, incompletely exposed, is a flat, hemicircular disc (?*p*, Fig. 33). Although poorly preserved, the edge which Parrington (1939: fig. 2) reconstructed as straight is in fact somewhat concave and therefore the pisiform was probably crescentic in outline. In *Diademodon* (*p*, Fig. 34A) the pisiform is also crescentic but its posteromedial margin (as illustrated, not necessarily its true orientation) is swollen. As with the pisiform of *Thrinaxodon* the articular relationship of this bone remains in doubt. In *Leavachia* the pisiform is a flat, round disc (Broom, 1948: 625).

Two centralia are known to be present in the complete carpus of *Thrinaxodon* (UMC R.2733; Fig. 33) but their precise identity is uncertain because of disarticulation. An acid-prepared but incomplete carpus of *Thrinaxodon* (SAM K.1395) shows two cylindric nodules lying distal to the radiale and intermedium, with their long axes oriented transversely to the long axis of the manus. If these are centralia, as their position would indicate, and if they are in actual articulation, then the restoration given by Parrington (1939: fig. 2), with the long axis of the lateral centrale parallel to that of the foot, is incorrect. Tentatively accepting the identification and orientation of these carpals in SAM K.1395, the following description is given. The medial and smaller of the two centralia is slightly dorsoventrally compressed. The cylindric posterior surface articulates with the transverse anterior groove of the radiale; the anterior surface bears a depression for articulation with distal carpal I. The lateral centrale is wider distoproximally and less dorsoventrally compressed than the medial, giving it a truly cylindrical appearance. In mediolateral width both centralia are equal. The only obvious articular surface on the lateral centrale is a rather vertical, round facet on its posterior aspect, evidently for articulation with the intermedium. In *Leavachia*, Brink and Kitching (1953a: 314) find that the medial centrale and radiale are fused, contrary to Broom's description (1948: 624–625).

The carpus of *Thrinaxodon liorhinus* figured diagrammatically by Broom (1932b: fig. 91) has only four distal carpalia, the fourth and fifth presumably being fused. Parrington (1933: 18–19) described and later (Parrington, 1939) figured a specimen (UMC R.2733) in which the fifth distal carpal was preserved as a small but separate element. The discrepancy between the two accounts may be tentatively settled in Parrington's favor because the specimen figured by Broom is unidentified and was later admitted to be unsatisfactorily preserved (Broom, 1936: 405). However the possibility that ossification varied with age or some other factor cannot be wholly discounted when so few determinable specimens are known. The morphological detail of the distal carpalia are not determinable from UMC R.2733 because of incomplete ossification. All are somewhat nodular and Parrington's (1939: fig. 2) assessment of their relative sizes is probably correct: I > IV > III > II > V. In *Diademodon* (Fig. 34A) there are apparently only four distal carpalia, with loss or fusion of V. All are nodular, except I which is flat and plate-like. In dorsoventral view their relative sizes are the same as in *Thrinaxodon*. In *Leavachia* also there are probably only four distal carpalia, although Brink and Kitching (1953a: 314) find that the second carpale is missing in the type specimen. There is a possibility, in view of the double facet on the distal end of the fused medial centrale and radiale, that *Leavachia* possessed only three distal carpalia, i.e., I, (II lost or fused), III, IV, (V lost or fused). Brink and Kitching's figure shows the fused centrale-radiale apparently in place and articulating with distal carpale I medially and metacarpal II laterally.

METACARPUS.

MORPHOLOGY. A complete metacarpus is adequately known in *Thrinaxodon* (BPI 376) and poorly known in *Diademodon* (USNM 23352; Fig. 34A). The metacarpals are all an elongate dumbbell shape and vary significantly only in shaft length with IV > III > V > II > I. Viewed dorsally the metacarpals appear nearly symmetrical, the proximal ends flaring laterally somewhat less than the distal ends. Viewed laterally the metacarpal outline is asymmetrical because the proximal end is much thicker than the distal. The proximal articular facet is gently convex and rather square in outline, whereas the distal facet is flat and rectangular. A shallow depression on the proximolateral surface of all shafts except V accommodates the proximal end of the laterally adjacent metacarpal.

PHALANGES

MORPHOLOGY. Broom (1932b: 270) figured a manus of *Thrinaxodon liorhinus* as having the primitive reptilian digital formula of 2-3-4-5-3, with the second phalanx of digit III and the second and third phalanges of digit IV reduced to discs. Later Broom (1936: 405) accepted Parrington's (1933: 18–19; 1939: 211) finding that two articulated specimens (UMC R.2740) clearly had four phalanges in digits III and IV, in each case the second phalanx reduced to a plate-like disc. There is therefore no doubt that the correct digital formula for *Thrinaxodon* is 2-3-4-4-3. Considering the trend toward reduction of phalangeal number in *Lystrosaurus* zone cynodonts, it is not improbable that the larger cynodonts of the *Cynognathus* zone achieved a "mammalian" count of 2-3-3-3-3. Phalanges of both *Cynognathus* and *Diademodon* are known from two collections (BPI 1675, NMB C.2709) made from separate localities where disarticulated remains of these genera are preserved together. It is not possible, however, to distinguish morphologically two types of phalangeal elements and on the present small sample it must be concluded, barring size parameters, that homologous phalanges of these genera are identical. No disc-like, reduced phalanges were recovered in either of these collections which include many fragments as small as or smaller than the expected size for such elements. Sampling error does not account for their absence and thus there is circumstantial evidence that *Cynognathus* and *Diademodon* had a phalangeal formula of 2-3-3-3-3. The partially disarticulated manus of *Diademodon* (USMN 23352; Fig. 34A) preserves only digit III in which there are three phalanges. Crompton (1955b: 626–627) concluded that the middle Triassic cynodont *Cricodon metabolus* probably possessed a phalangeal count of 2-3-3-3-3. Thus the preponderant evidence indicates that at least several genera of advanced cynodonts had achieved a mammalian phalangeal number.

Brink and Kitching (1953a: 314) reported that the phalangeal count in *Leavachia duvenhagei* (RC 92) is 2-3-3-4-3, not 2-3-4-4-3 as Broom (1948: 626) claimed.

The detailed description of individual phalanges given below is based on the BPI 1675 collection of disarticulated, intermixed skeletons of *Cynognathus* and *Diademodon* with supplementary data from another similar collection (NMB C.2709). Not only is it impossible to separate the phalanges generically, but also there is no known feature with which to distinguish manual from pedal phalanges. The lack of variation in the known sample makes it probable that *Cynognathus* and *Diademodon* phalanges are very similar. Furthermore the manual phalanges of *Diademodon* (USNM 23352) and *Thrinaxodon* (SAM K.1395) compared to the pedal phalanges of a generically unidentifiable Middle Triassic cynodont (BMNH TR.8) show that there is little basic morphological difference between analogous fore- and hindfoot elements. Therefore until better material is available the following description applies to manual as well as to pedal phalanges.

Proximal phalanges (Fig. 35I-L) are all uniformly hourglass-shaped and approximately in the same proportions. In dorsal view (Fig. 35I) the proximal half of each expands gradually from a moderately constricted waist to a proximal terminus bearing a vertical, oval articular facet (*pr ar f*, Fig. 35L). The distal half flares abruptly to a hemispherical terminus where the crescentic, convex articular facet is inclined anteroventrally at an angle of about 45° to the long axis of the bone (*di ar f*, Fig. 35J,K).

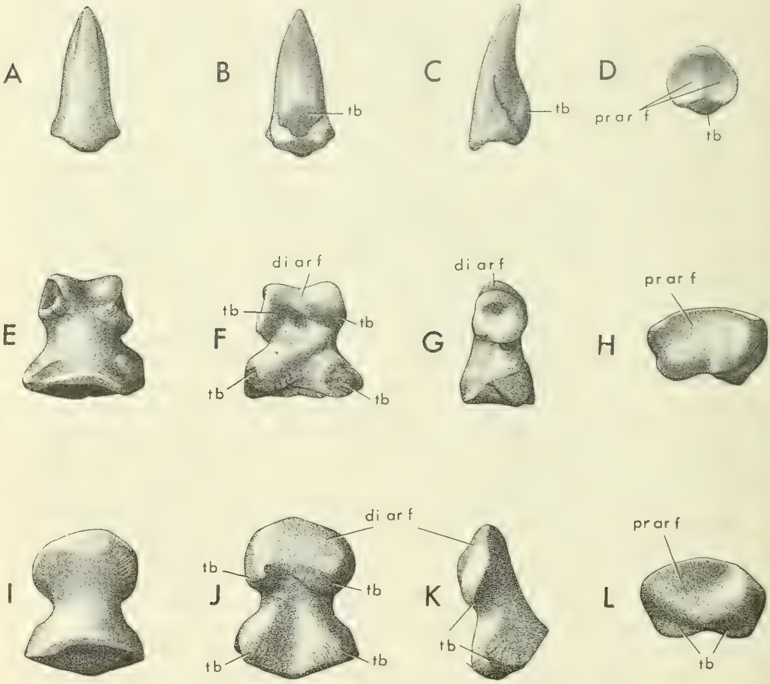


FIG. 35. Isolated phalanges of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, A–D, distal phalanx; E–H, penultimate phalanx; I–L, proximal phalanx, in (left to right) dorsal, ventral, lateral and proximal views. These elements are not necessarily from the same individual and may represent either manual or pedal phalanges, or both. X1.35. Abbreviations: *di ar f*, distal articular facet; *pr ar f*, proximal articular facet; *tb*, tubercle for ligamentous, tendinous or capsular attachment.

On the ventral surface are four tuberosities situated at the "corners" where an articular surface adjoins the ventral surface (*tb*, Fig. 35J,K); these probably functioned in attachment of ligaments or digital flexors. Striations adjoining the proximal and distal ends mark ligamentous or capsular attachments. In *Thrinaxodon* and *Galesaurus* the phalanges are longer relative to the waist diameter but are otherwise similar in morphology to those of *Cynognathus* and *Diademodon.*

Penultimate phalanges, disregarding the vestigial discs of III and IV, are also uniformly hourglass-shaped and approximately in the same proportions (Fig. 35E-H). The width of the distal terminus is somewhat less than that of the proximal. The oval proximal facet, indented along the median sagittal plane, is almost vertically oriented; it faces slightly dorsally (*pr ar f*, Fig. 35H). Articulation with the inclined distal facet of the proximal phalanx (or vestigal disc) must have normally been at an angle of about 135°. In a specimen of *Galesaurus* (SAM K.1119) two of these phalanges are preserved in articulation at an angle of 115°; however this probably represents the flexed condition common to rigor mortis. The distal end of the penultimate phalanx is essentially a cylinder, the two ends of which are concave and face slightly anterodorsally. The articular surface for the ungual phalanx is a pulley-like groove extending in an arc of almost 270°, thus permitting considerable flexion and extension of the claw (*di ar f*, Fig. 35F,G). The four corners of the ventral surface (Fig. 35F) each bear a rugose tuberosity; frequently they are asymmetric and unequal in size. The dorsal surface also bears asymmetric tuberosities at its proximal corners. The penultimate phalanges of *Thrinaxodon* and *Galesaurus* are morphologically similar to those of *Cynognathus* and *Diademodon.* Proportionally they are longer relative to their width and are thus comparatively more slender.

Cynodont ungual phalanges are slender, tapering cones with little ventral curvature (Fig. 35A-D). The distal half is somewhat dorsoventrally compressed. The articular facet is a round concavity divided sagittally by a raised median ridge (*pr ar f*, Fig. 35D) in larger cynodonts. The dorsal and ventral edges of ungual facets are extended posteriorly to form distinct lips which fit snugly into the opposing pulley-like groove of the penultimate phalanx. At the proximal base of all ungual phalanges is a tuberosity for a flexor muscle insertion (*tb*, Fig. 35B-D). There appears to be little variation among cynodont unguals, but in one complete pes (BMNH TR.8) the unguals are flatter and less pointed than in any other known unguals.

3. FUNCTIONAL CONSIDERATIONS OF THE PECTORAL GIRDLE AND FORELIMB

INTRODUCTION

The significance of the cynodont postcranial skeleton to the evolution of mammals can only be understood in functional terms. Functional analyses usually treat three different but interrelated aspects: 1) the normal position and orientation of skeletal parts to each other, (e.g., in the case of the appendicular skeleton, the stance or habitual stationary posture) ; 2) the changes in position and orientation of skeletal parts during normal activity, again with respect to the appendicular skeleton, the gait or excursion of the limbs; and 3) the adaptive significance and relative efficiency of (1) and (2). If fossil material is considered, the fundamental difference between these functional aspects relates to the probability of approximating the truth in each case. For instance the stance of a fossil tetrapod is more confidently reconstructed than its gait because only basic articular relationships need be established. An interpretation of limb movement further requires evidence of muscular and ligamentous systems which often have no close analogy among living forms. The evaluation of a system's adaptive nature and relative efficiency still further requires physiological as well as paleoecological evidence which is always incomplete. Thus I regard conclusions on these three aspects with confidence decreasing (1) to (3), although I nevertheless will draw conclusions relating to each aspect.

The Shoulder Girdle of Cynodonts and the Evolution of the Mammalian Shoulder Girdle

An evaluation of the cynodont shoulder girdle in terms of the evolving mammalian shoulder girdle must take into account its basic function and mechanics. The function, of course, has remained essentially unchanged throughout tetrapod evolution: to form a stable "base" for the forelimbs which will transmit both the weight of the body and the locomotory thrust of the limbs. The mechanics of pectoral girdle function have undergone radical changes which will be discussed in this and the following section.

Romer (1922a, 1922b; see other authors cited by him) discussed the derivation of the mammalian pectoral girdle from that of primitive tetrapods. His primary concern, however, was to establish certain nervous, muscular and osteological homologies in the pectoral girdle complex of diverse living and fossil groups. Since his work, general reviews of pectoral girdle evolution have been published by Lessertisseur and Sigogneau (1965), Lessertisseur and Saban (1967) and Jouffroy and Lessertisseur (1967), but no attempt has been made to evaluate the biomechanical factors involved.

One of the fundamental problems in pectoral girdle evolution is to explain the modification of its various constituent bones in the course of the reptilian-mammalian transition. The clavicles and (posterior) coracoids are reduced in size, the latter becoming vestigial. The anterior (epi- or pro-) coracoids are, with the exception of monotremes, lost altogether. The scapulae, as Romer has shown, are remodeled by dorsal migration of musculature originally associated with the coracoid plate. The history of these complex changes is not fully known and even if it were the explanation probably would not be simple. However, as a first approximation the following analysis attempts to relate known or inferred mechanical facts to the general tendency toward pectoral girdle diminution in the ancestral mammalian lineage. The biomechanical principles employed are derived primarily from the classic work of James Gray (1944), "Studies in the mechanics of the tetrapod skeleton."

Gray (1944: 102) demonstrated that static support of the body involves employment of limbs (and girdles) as struts, whereby a limb "exerts forces along its own mechanical axis only, the moment of muscular tensions operating about the hip or shoulder joint being zero". For instance graviportal mammals are capable of aligning their limbs more or less vertically beneath the body (Fig. 36A, A'). In such a case the axial thrust of the limb due to body weight (W) is countered by an equal but opposite vertical resistance (R) at the ground. The vectorial path traveled by these forces, i.e., the mechanical axis (MA, Fig. 36), corresponds in this case to the morphological axis (MOA, Fig. 36), which is composed of the series of skeletal elements transmitting the forces. If the animal remains stationary, neither transverse or longitudinal moments of resistance are generated and the system is theoretically resolvable into a two component system of W and R. However, such simplicity of design is probably never achieved by any tetrapod because limb bones and girdles are not simple linear axes nor are the muscles and ligaments which stabilize them symmetrically arranged. Nevertheless the concept of morphological (limb) and mechanical (force) axes—the former determining the orientation of the latter are useful in investigating relationships of limb form and function.

All tetrapod limbs are segmented and each segment is capable of variable degrees of independent position and movement. To be more precise, the morphologic axis changes course at joints. Since this is the case, transverse, longitudinal or both forces may be introduced which must be balanced by equal but opposite forces if the animal is to hold a static posture. In Figure 36B the elbow joint is bent outward in a plane perpendicular to the sagittal plane. The morphological (MOA) and mechanical (MA) axes are separated at all but two points, i.e., at the glenoid (G) and base of the foot. In such a case the transverse and vertical moments of resistance are determined from a vector analysis of the mechanical axis (MA). Each of the opposing forces (W, R) imparted along the mechanical axis has a vertical (Wv, Rv) and a transverse (Wt, Rt) component. For stationary stability,

$$Wt = Rt = Wv \tan a$$
$$Wv = Rv$$

where angle a is the angle between the mechanical axis and a parasagittal plane. The vertical components represent the gravitational interaction of the body weight and substrate. The horizontal component Rt represents frictional resistance of the foot applied laterally against the body. This resistance must be opposed by an equal force generated by the contralateral foot and transmitted by the body. The force opposing Rt may be regarded in terms of Wt, the resistance of the pectoral girdle and thorax to compression or, to put it differently, the competence of the pectoral girdle and thorax in transmitting the force generated by the contralateral foot. As angle a increases or decreases, so also do the horizontal components relative to vertical if equilibrium is to be maintained. An increase in the horizontal components requires structural adaptations in the shoulder girdle to resist thoracic compression and to transmit the equal but opposed forces from contralateral feet.

In Figure 36B the elbow joint is bent backward in a parasagittal plane. As in the previous case horizontal moments of W and R are introduced, but instead these act in a parasagittal and and not a transverse plane. Frictional force generated at the base

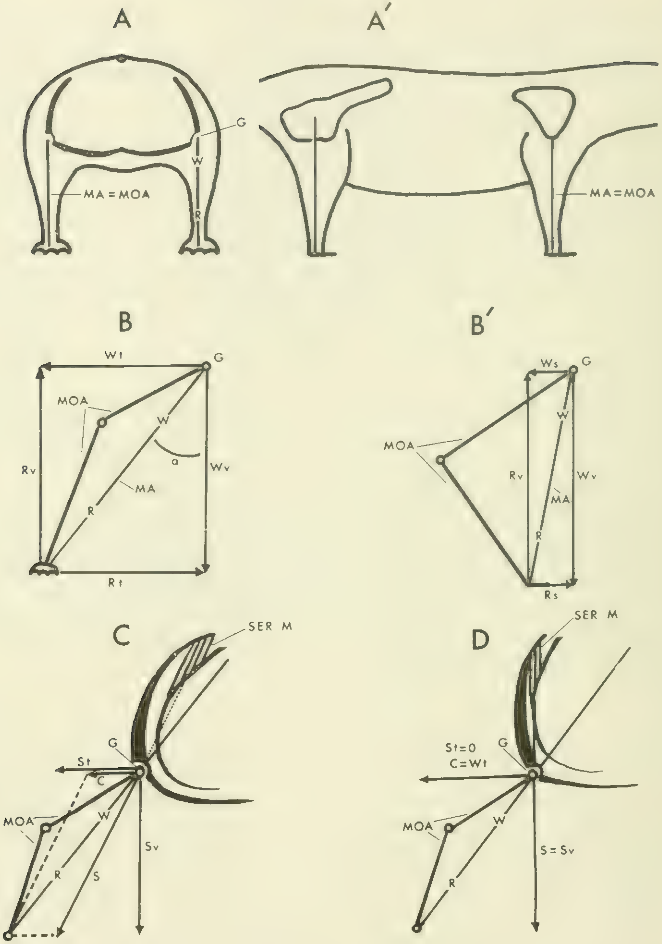

A
A′
G
W
MA = MOA
R
MA=MOA
B
B′
Wt
G
MOA
W
a
Rv
Wv
MA
R
Rt
Ws
G
W
MOA
Rv
Wv
MA
R
Rs
C
SER M
G
St
C
MOA
W
R
S
Sv
D
SER M
St=0
C=Wt
G
MOA
W
R
S=Sv

FIG. 36. Diagrammatic representation of the mechanics of tetrapod limbs, partly after Gray (1944). A, transverse section through shoulder girdle and limbs of a tetrapod. A′, parasagittal section through the same. B, B′, transverse and parasagittal sections through the shoulder girdle and forelimb of tetrapods in which the forelimb is held laterally and parasagittally, respectively. C,D, transverse sections through the shoulder and forelimb of tetrapods in which the limbs are held laterally in the same manner but in which the orientation of the scapula and serratus musculature varies. *G*, glenoid; *MA*, mechanical axis of limb; *MOA*, morphological axis of limb; *SER M*, serratus muscle. For other abbreviations and explanation, see text.

of the foot (*Rs*) is balanced by an equal but opposite force (*Ws*) at the shoulder girdle. *Ws* represents the resistivity of the shoulder girdle to independent forward displacement. Ultimately the equilibrium of the couple *Ws-Rs* depends upon an equal but reversed couple on the ipsilateral hind foot. In most tetrapods the orientation of the limb is such that both transverse (*Wt*, *Rt*) and parasagittal (*Ws*, *Rs*) components are introduced; the result is conceptually complex, but the principles involved are of course the same.

From the above examples it is sufficiently clear that limbs held away from the body axis in the so-called "sprawling position" must produce a large transverse, or compressive, component acting on the thorax. The massive, conjoined pectoral girdles of primitive tetrapods appear to have been an adaptation to sustain the compressive forces generated by sprawling limb posture. In particular the broad coracoid plate may have aided in dispersion of these forces over a relatively large area of the thorax, while the massive clavicles and interclavicle were effective transmittors of these forces to the contralateral foot. Reduction of the pectoral girdle could only follow proportional reduction of the compressive component.

In the foregoing hypothetical models the role of the scapula in transmitting forces was neglected for the sake of simplicity. Nevertheless the orientation of the scapula and other girdle elements determines to a large extent the stresses which the limbs must bear. Gray (1944: fig. 19) pointed out that the interaction of *R* and *W* at the glenoid may be analyzed in terms of the orientation of the Mm. serrati which are probably the most important muscles uniting the anterior half of the body with the scapula. His argument may be briefly restated with reference to Figure 36C, diagrammatically illustrating a transverse section of a tetrapod in which the limb is held perpendicularly to the long axis of the body. The scapular blade is inclined medially and is somewhat bowed, with the result that the Mm. serrati on the average are inclined ventrolaterally. *W* is the resultant of force *S* of the body weight transmitted to the scapula by the serratus musculature and force *C* tending to displace the scapular base laterally. The horizontal component of *S* is *St* and

$$St + C = Wt.$$

Gray did not pursue this argument to its conclusion, viz., that the transverse force *Wt* (as in Fig. 36B) is no longer wholly dependent upon the structural competence of the shoulder girdle to resist compression. The girdle is designed to generate its own laterally directed force, *St*. Limb proportion and orientation which result in larger *Rt* values may then be associated with a relatively weaker pectoral girdle. Such an arrangement seems to have been developed among the cynodonts and apparently persists in a somewhat modified form among monotremes as well. The cynodont scapula is bowed laterally to a marked degree (Figs. 17C,D; 18C,D), hence orienting the serratus musculature in the manner suggested above. Such an arrangement might have been a contributing factor in the reduction of the coracoids and clavicles from the more massive, primitive condition. The fossorial habits of monotremes and the extremely sprawling position of the humerus may have necessitated both the inclination of the scapula and the retention of the primitive, robust coracoid-clavicular complex.

Whether or not the position of the monotreme scapula is due to fossorial specialization, it remains a strong possibility that the curvature of the cynodont scapula is related to the reduction of transverse, compressive forces acting on the thorax. There is no question that the coracoid plates and clavicles are significantly reduced in size over those in pelycosaurs and early therapsids.

In Figure 36D the stance remains the same as in Figure 36C but the Mm. serrati are disposed vertically so that the horizontal component (St) of S is nil. The lateral component (Wt) of W now is accounted for only in terms of C, the lateral force resisting compression of the girdle. All other factors being equal between Figure 36C and D the pectoral girdle of D must have structural adaptations to resist that part of the Rt compressive force opposed by St in C. In other words the pectoral girdle of D must be stronger than that in C in order to make up for the less advantageous mechanical position of the serrati in resisting compressive forces. Such an arrangement is characteristic of pelycosaurs and other early tetrapods in which a massive shoulder girdle and vertical scapular blades are developed.

Gray (1944: fig. 19) concluded by simply noting that "if the line of action of the serratus tension does not pass through the glenoid, other external forces—active or passive—must act on the girdle in order to prevent the latter rotating inwards or outwards about the head of the humerus." If the line of action passes medial to the glenoid, as, for instance, it must in living crocodilians, the compressive effect of Rt is increased by Wt. This may be withstood by structural adaptations of the rib cage to resist deformation as well as by strengthening the shoulder girdle. This condition is not common to mammals, however, nor is the condition in which the line of serratus action passes lateral to the glenoid. In most mammals the lines of serratus action are aligned nearly vertically and scapula so closely approximates a parasagittal plane above the limb that only minor transverse forces are generated. With the exception of the condition in monotremes (see above) the mammalian coracoid plate is reduced to a small vestige for muscular attachment. The clavicles, also much reduced in size, still stabilize the scapula, as in primitive forms, but serve only a fraction of the original requirement. Thus part of the history of the mammalian pectoral girdle can be interpreted in terms of changes in forelimb position—the subject of the next section.

THE GLENO-HUMERAL ARTICULATION AND FORELIMB MOVEMENT

The mammalian glenoid is typically formed by a shallow, more or less circular glenoid cavity which faces ventrally. The cavity is surrounded by a fibrocartilaginous glenoid labrum which somewhat deepens the cavity, forming a rounded socket for reception of the humeral head. In primitive tetrapods the glenoid was neither circular nor ventrally facing, but had a peculiar, twisted morphology, best described as screw-shaped, and faced laterally. The derivation of the mammalian pattern involved not only major morphological modifications but also postural and functional changes as well. In order to evaluate cynodonts as an intermediate stage the primitive arrangement, i.e., in pelycosaurs, must be fully understood.

PELYCOSAURS

The screw-shaped glenoid common among Paleozoic tetrapods has been discussed by Watson (1917a), Romer (1922b), Miner (1925) and Haines (1952), each of whom supposed that its intricate morphology permitted accurate reconstruction of humeral movement. Nevertheless there is surprisingly little agreement among these authors on movements of the humerus. No evaluation of the functional advantage of a screw-shaped glenoid has even been given. Yet the persistence of this structure among pelycosaurs and primitive therapsids (Deinocephalia) renders it fundamentally important to the understanding of synapsid forelimb evolution. The morphology of the forelimb and pectoral girdle of the Pelycosauria, thoroughly documented by Romer and Price (1940), will not be redescribed here except where required to clarify functional analysis. *Dimetrodon* may be taken as representing a primitive synapsid condition; the small amount of morphological variation in the forelimb skeleton of pelycosaurs makes it unnecessary to consider other forms. Before presenting my conclusions concerning the early evolution of the glenoid and forelimb movement, the contributions of previous authors will be considered.

Watson (1917a: 13 ff.) attempted to reconstruct *Dimetrodon* forelimb mechanics on the basis of articular relationships and inferred musculature. He concluded that the humerus, held at right angles to the sagittal plane, lay nearly parallel to the ground, that it could not have been advanced much beyond the right angle position, but that it could have been retracted posteriorly as much as 50°. Watson estimated that in "normal position" (normal stance?) the antebrachium would lie at a 30° angle to the ground. He further concluded that the antebrachium was restricted in transverse movement, i.e., movement parallel to a vertical plane through the humeral axis, by the deep sigmoid notch of the ulna, but that a limited amount of anteroposterior movement was made possible by "the spheroidal shape of the ulnar articulation." In Figure 37 a *Dimetrodon* right forelimb and pectoral girdle are diagrammatically illustrated to show phases of the locomotory cycle as interpreted from Watson's (1917a) description. In Figure 37 (A, A′, A″) the humerus is parallel to the ground and at right angles to the body; the forearm is at an angle of 30° to the ground and essentially parallel to the body. From this position the humerus is retracted and slightly depressed and the elbow is flexed to give a position as in Figure 37 (B, B′, B″). Simultaneously the humerus is rotated on its long axis (depressing the anterior and elevating the posterior aspects of the bone) to permit elevation of the antebrachium. The combined action of these movements advances the pectoral girdle, but at the same time moves it dorsolaterally toward the foot. Figure 37 (C, C′, C″) and (D, D′, D″) depict the completion of the cycle whereby "the whole anterior part of the body is . . . swung from side to side at each stride."

Romer (1922b: 548–550) also recognized that humeral action in primitive tetrapods required, in addition to the principal anteroposterior movement, abduction and adduction (raising and lowering) as well as long axis rotation. However he objected to Watson's apparent assumption that the screw-shaped glenoid represents a single articular facet. Romer pointed out that the opposing facets would therefore represent segments of rather large circles and that "any motion of more than 20° would cause the humerus to cut the muscular surfaces at the anterior and posterior edges of the joint." He furthermore concluded that such an arrangement would generate excessive friction. Instead, Romer proposed that both humeral head and glenoid bore two "partially separated" facets, one anterior and one posterior (see also Romer and Price,

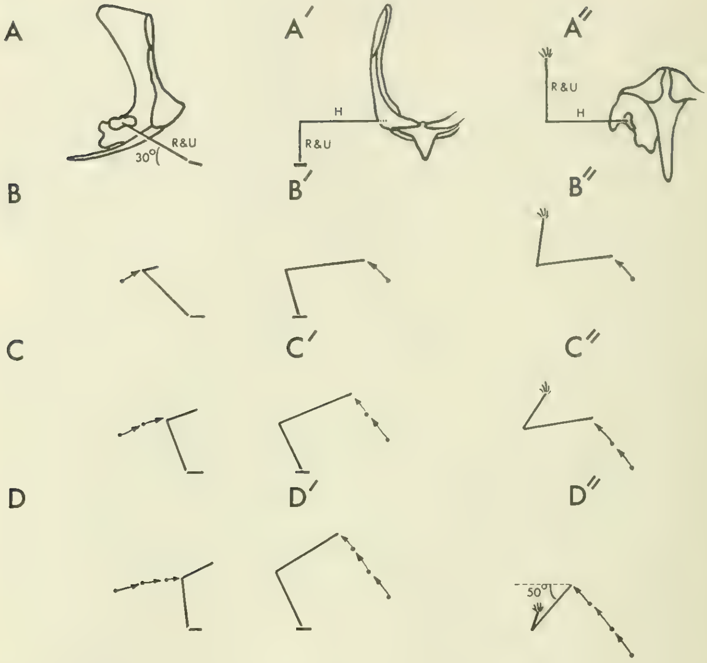


FIG. 37. Diagrammatic representation of forelimb movement in *Dimetrodon* as proposed by Watson (1917a). From left to right: lateral, anterior and ventral views. A, A′, A″ represent the start of the propulsive stroke; D, D′, D″ the completion of the propulsive stroke. *H*, humerus; *R & U*, radius and ulna.

1940: 138). His evidence for such a division—a slight ridge on some humeri and a contraction in the outline of the glenoid—is dubious at face value and since no functional explanation is given, the concept renders the screw-shaped glenoid even more enigmatic. Moreover two separate surfaces, as proposed by Romer, would virtually prohibit any movement but simple abduction and adduction. Anteroposterior movement is prohibited by the interference of adjacent facets. I conclude from an examination of well-preserved humeri and glenoids that there is no reliable evidence of separate facets and that, as will be shown in detail below, the complex morphology of the screw-shaped glenoid and spiral humeral head are related to diverse functional requirements of a single articular joint.

Miner (1925: 165–168) described in detail the glenohumeral articulation in *Eryops*. According to his interpretation the humeral head articulates with the posteriorly facing, anterior half of the glenoid when the humerus is in its posterior position at the end of the propulsive stroke. As the humerus is brought forward again, the head slides posteriorly along the glenoid surface and reaches the dorsolaterally facing, posterior half of the glenoid at the completion of the recovery stroke. In addition to the sliding action of the joint Miner claimed that humeral movement entails a long axis rotation of about 90°. Watson (1917a: 3) had previously denied the possibility of long axis rotation in *Eryops*. He interpreted the screw-shaped glenoid and humeral head as fitting so snugly that humeral movement was restricted to a small amount of anteroposterior movement with a minor dorsoventral component. However Watson's description did not take into account the cartilage that undoubtedly covered both surfaces during life; such a cartilaginous cap would in effect separate the apparently interlocking bony surfaces. Therefore accepting Miner's view, longitudinal rotation of the humerus is part of primitive forelimb function.

Finally Haines (1952: 419–421) attempted to reconstruct the movements of the humerus in *Dimetrodon* taking into consideration the action of supposed cruciate ligaments. A dorsal and a ventral pair of these ligaments, arranged in an "X" pattern across the glenohumeral articulation, are common among living lizards. Haines concluded that movement of the distal end of the humerus "followed a roughly circular track" similar to that exhibited by lizards and urodeles. However Haines did not work with any fossil material, his conclusions on *Dimetrodon* being based on a paper and paste model constructed from published figures. Therefore it is difficult to accept his contention that two such utterly disparate glenohumeral joint types as that of *Dimetrodon* and modern lizards should be functionally the same. In fact there is no osteological evidence that pelycosaurs possessed cruciate ligaments, but even supposing they did, Haines admits that "slight changes in the lengths or positions of these ligaments may make great differences in the movements." While cruciate ligaments are critical regulators of humeral movement in the relatively simple "ball and socket" type joint of some living reptiles, the pelycosaurian shoulder mechanism is at least partly defined by the intricate morphology of the glenoid—irrespective of the accessory support of ligaments and glenoid capsule.

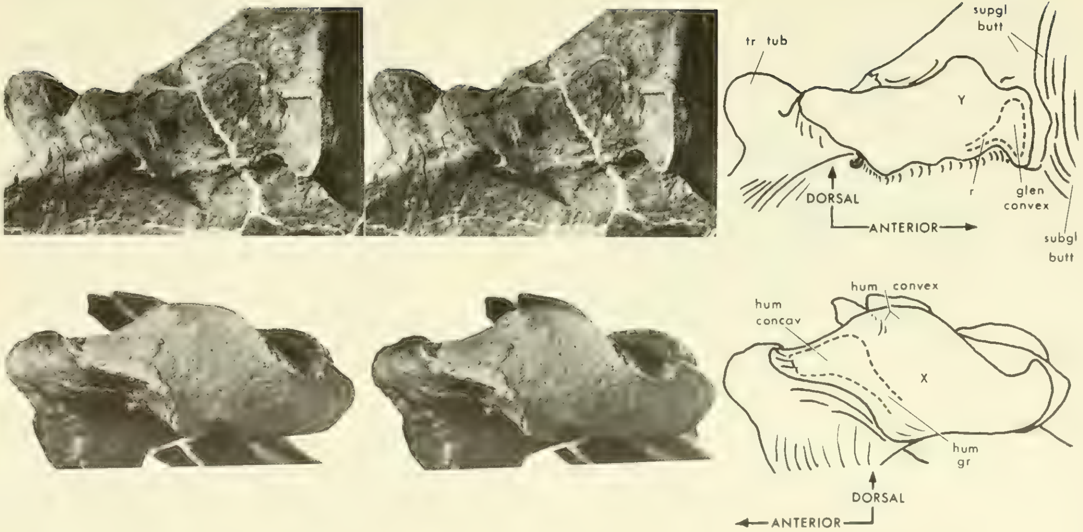
My conclusions on pelycosaur forelimb mechanics are based primarily on an unusually well-preserved scapulocoracoid and humerus of an adult *Dimetrodon* sp. (MCZ 3357) from the Belle Plains Formation of Texas. Unlike much pelycosaur material the bone is undistorted and preserves detailed textural features. Morphological details were verified insofar as possible in other specimens (MCZ 2951 and YPM 661 in particular).

The glenoid in *Dimetrodon* is about 15 to 20 percent shorter anteroposteriorly than the humeral head facet. In MCZ 3357, for instance, the glenoid is 61 mm long and the humeral head 73 mm; there is no reason to interpret the glenoid as having been longer by virtue of cartilaginous overgrowth without also supposing the humeral head was likewise increased in length. The fact that the humeral facet is longer anteroposteriorly than the glenoid facet is prima facie evidence for anteroposterior movement of the humerus along an essentially horizontal track as postulated by Watson. Such a movement could not have taken place by means other than a sliding of the respective articular surfaces on one another, the mechanism proposed by Miner for *Eryops*. According to this view the anterior end of the humeral facet passes beyond the anterior limit of the glenoid as the humerus is retracted; conversely, as the humerus is brought forward, the posterior end of the humeral facet passes beyond the posterior limit of the glenoid. Romer (1922b: 549) claimed that such facet displacement would sever adjacent muscular and ligamentous tissues and entail excessive friction as well. But Miner (1925: 167–168) correctly pointed out that among living tetrapods the surface area of the humeral head is usually larger than that of the glenoid socket. The displacement of part of the humeral articular facet from the glenoid surface follows the obvious principle of any "ball-and-socket" type joint. In living tetrapods, and presumably in fossil forms as well, the articular capsule and adjacent musculature are arranged so as not to be strained during normal movements.

Watson (1917a) correctly surmised that the propulsive and recovery strokes of the humerus in *Dimetrodon* involve more than simple anteroposterior swing, although he failed to present any morphological evidence for his rather specific conclusions. During the propulsive stroke depression (or adduction) and long axis rotation occurs. Evidence for such movements is derived from the reorientation of articular contacts which must occur if the humerus is to preserve the sliding articulation previously shown to be necessary. Since the changing interrelationships are conceptually complex to present, attention will be focused initially on the anterior aspects of the humeral head and glenoid.

The anterior quarter of the glenoid faces primarily posteriorly, but also slightly laterally and, if the scapular orientations given by Romer and Price, 1940, are correct, ventrally. The surface bears a low convexity (*glen convex*, Fig. 38) which falls away in all directions except posteroventrally where it tapers to a gradually attenuating ridge (*r*, Fig. 38). The corresponding anterior quarter of the humeral head is slightly concave and faces dorsomedially. This concavity (*hum concav*, Fig. 38) is continued as a very shallow groove (*hum gr*, Fig. 38) posteroventrally along the ventral margin of the facet. When the humerus is in its most anterior position the glenoid convexity and humeral concavity fit together; the latter is so oriented that in order to key with the former the distal end of the humerus must be slightly elevated (relative to the proximal end) and its distal ventral surface brought to face anteroventrally. In such a position the antebrachium is directed anteriorly to begin the propulsive stroke (Fig. 39A). As the humerus is retracted the glenoid convexity (together with its posteroventral ridge) loses contact with the humeral concavity but follows, as on a track, the groove extending posteroventrally along the humeral head. In other words the humeral concavity leaves the glenoid convexity by sliding forward as the distal end of the humerus moves back. But the proximal end of the humerus cannot slide directly forward without the glenoid convexity encountering a similar convexity on the humerus (*hum convex*, Fig. 38). The path of least resistance, therefore, lies along the shallow groove which winds posteroventrally around the head to reach the ventral surface of the humeral head. In order for the glenoid convexity to follow this groove, the humerus must be rotated anteroventrally and at the same time depressed. The rotation causes the distal, ventral surface of the humerus, which at the beginning of the stroke faces anteroventrally, now to turn ventrally, permitting elevation of the antebrachium (Fig. 39B).

At the completion of the stroke the most ventral sector of the humeral groove abuts against the glenoid convexity. The humeral concavity is displaced anteroventrally and is out of contact with the glenoid.


tr tub
supgl butt
Y
r
glen convex
subgl butt
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hum convex
hum concav
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hum gr
DORSAL
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FIG. 38. Stereoscopic photographs of the glenoid (top) and proximal end of the humerus (bottom) of *Dimetrodon sp.* MCZ 3357. X0.7. Abbreviations: *glen convex*, glenoid convexity; *hum concav*, humeral concavity; *hum convex*, humeral convexity; *hum gr*, humeral groove; *r*, ridge; *subgl butt*, subglenoid buttress; *supgl butt*, supraglenoid buttress; *tr tub*, tubercle for the coracoid head of the triceps; *X*, *Y*, points of contact during the final stage of the propulsive phase.

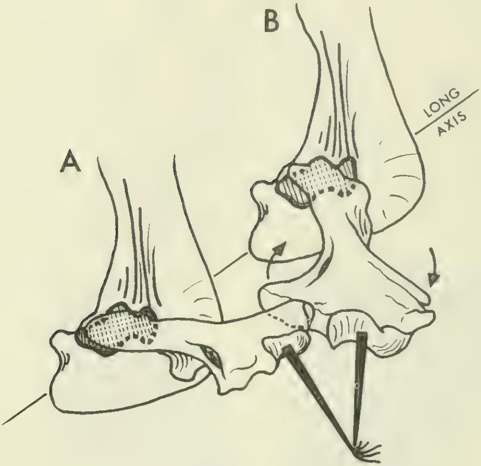

FIG. 39. Diagrammatic reconstruction of the scapulocoracoid and forelimb of a walking pelycosaur viewed from the posterolateral aspect. A, the beginning of the propulsive phase, with the antebrachium directed forward; B, the completion of the propulsive phase, with the humerus rotated (arrows) on its longitudinal axis to permit elevation of the antebrachium. *Long axis*, longitudinal axis of the body.

The remainder of the glenoid and humeral head facets are constructed to facilitate the humeral movements described above. The posterior half of the glenoid is a broad shelf which faces dorsolaterally and slightly anteriorly (Fig. 38). This half merges with the anterior half of the glenoid across a surface which is nearly vertical and faces laterally and, more anteriorly, posterolaterally. The posterior half of the humeral head is a strap-shaped surface, convex both dorsoventrally and anteroposteriorly (Fig. 38). This surface, facing medially and slightly ventrally, contacts the posterior half of the glenoid at the beginning of the stroke. Since the humeral surface does not face so much ventrally as does the glenoid surface dorsally, the humerus must be slightly elevated for the two surfaces to make even contact. At the completion of the stroke the posterior sector of the strap-shaped humeral facet is rotated dorsally out of contact with the glenoid. Simultaneously the anterior sector of the strap-shaped surface (*X*, Fig. 38) is brought into contact with the center sector of the glenoid (*Y*). This brings the broadest surface of the humeral head into contact with the most strongly buttressed part of the glenoid during the completion of the propulsive phase when propulsive forces are maximal.

Mechanically the screw-shaped design of the primitive glenoid served two functions in early tetrapod terrestrial locomotion: longitudinal rotation of the humerus and distribution of propulsive forces. The adaptive significance of a screw-shaped glenoid with respect to humeral rotation and propulsive forces will be evaluated separately.

Longitudinal rotation of the humerus, as Romer (1922b: 548) suggested, is required to preserve the humero-antebrachial articulation during locomotion. Among primitive tetrapods flexion and extension permit independent movement of the antebrachium relative to the humerus in a transverse plane, but the nature of the primitive trochleo-capitular joint conjoins the humerus and antebrachium in any movement in a parasagittal plane. Thus as the humerus moves from a position behind the antebrachium (at the beginning of a stroke, see Fig. 37A″) to a position more or less on line with the antebrachium (at the end of a stroke, see Fig. 37D″), the capitulum, for instance, must rotate from an anteriorly directed to a ventrally directed position. The persistence of the screw-shaped glenoid in face of the obvious alternative of a simple ball-and-socket joint, eventually evolved independently by reptiles and mammals alike, might be explained by its functional advantage to a system in which neuromuscular control for terrestrial locomotion was only primitively developed. The screw-shaped glenoid and spiral humeral head provide set trackways, so to speak, along which the joint must function. Minimal muscular coordination of complex simultaneous movements is required because the articulation effectively controls abduction or adduction as well as rotation once an anterior or posterior movement is initiated. Thus it appears that a possible lack of advanced neuromuscular coordination in the forelimb of primitive forms is compensated by the restrictive control of a specialized joint.

The glenoid of all tetrapods in addition to transmitting a portion of the weight to the forefoot must transmit to the body the propulsive forces generated by the limb. Propulsive forces are of course primarily anteriorly directed, although there is some reason to believe, following Watson (1917a: 14) and the functional analysis given above, that early tetrapods had a considerable transverse component as well. A glenoid formed on a laterally directed scapulocoracoid plate, as is the primitive pattern, is poorly suited to transmit forward propulsive forces to the body. Without structural adaptations to contain the propulsive force of the limb the resulting tendency would be to disarticulate the humeral head in an anterior direction. The screw-shaped glenoid accommodates the anterior propulsive force by means of its posteriorly directed anterior half (Fig. 38). The fact that the center of the glenoid faces as much laterally as posteriorly, in addition to the fact that there is a slight lateral inclination in the anterior half, probably reflects the presence of a substantial transverse component in the stroke as postulated above. These forces are further distributed to the scapulocoracoid via structural buttresses which reinforce the anterior half of the glenoid. The supraglenoid buttress (*supgl butt*, Fig. 38) is a thickened wedge of bone passing anterodorsally from the glenoid to the scapular blade. A similar feature, the subglenoid buttress (*subgl butt*, Fig. 38), passes anteroventrally to the procoracoid plate. Both structures reinforce that part of the glenoid receiving the main propulsive force or, in other words, distribute this force over the greater part of the pectoral girdle.

CYNODONTS

The cynodont shoulder girdle bears major structural changes from the pelycosaurian pattern that are indicative of a more functionally mammalian locomotor system. The most important changes involve reduction of the coracoid plates and modification of the glenoid. Vestiges of the pelycosaurian grade remain, however, such as the tuberosity for the triceps' coracoid head and the robust clavicles and interclavicle, and thus the cynodont shoulder girdle is a mosaic of advanced and primitive features. Few major changes are evident in the humerus and antebrachium which tend to be more conservative elements in early locomotor evolution. The most important modification of the humerus is in the loss of the spirally shaped head; in the antebrachium, the most salient characteristic is the increased robustness of both radius and ulna. A functional interpretation of the cynodont forelimb and girdle will be given after an evaluation of previous work.

Glenoid orientation and humeral position

Watson (1917a: 27 30) reconstructed the girdle orientation and limb action of a cynognathid, utilizing disarticulated and unassociated remains. He concluded that the shoulder girdle was inclined forward as in the echidna; that the glenoid cavity faces "outwards and backwards"; and that the humerus "normally" was carried parallel to the ground. There are inconsistencies to such conclusions and unfortunately Watson did not clarify his reconstruction by illustration. The cynodont scapula unquestionably does incline anteriorly, for in a vertical or posteriorly inclined position the procoracoid assumes an improbable position dorsal to the coracoid (also see Broom, 1948: 623). The question, therefore, concerns the degree of anterior inclination which in turn determines the glenoid orientation and consequently the humerus orientation. If the procoracoid-coracoid ventral margin is taken as parallel to the midventral line, as Watson seems to have implied, then the scapula inclines sharply forward (Fig. 40A). In such a position the glenoid is oriented posterolaterally, as Watson claimed, but also faces somewhat dorsally which clearly was not Watson's intention because the humerus must then be slightly elevated. Alternatively if the ventral margin of the coracoid plate is slightly elevated anteriorly and also turned medially to conform with the shape of the thorax, the glenoid faces posterolaterally but also somewhat ventrally (Fig. 40C). Watson did not account for the necessary ventral component of glenoid orientation because he apparently overlooked the ventral bowing in the proximal end of the humerus (see above, p. 113). If the humerus is articulated with a more or less horizontally facing glenoid, the ventral bowing would elevate the elbow above the glenoid level (Fig. 40B). This arrangement is very improbable because the antebrachium, articulating at right angles to the distal end of the humerus, would be forced into the strenuous position of an inclined, lateral strut (*dotted line*, Fig. 40B). In addition the loss of net length to the limb would elevate the body only a short distance from the ground. Alternatively if the glenoid is oriented to face slightly ven-

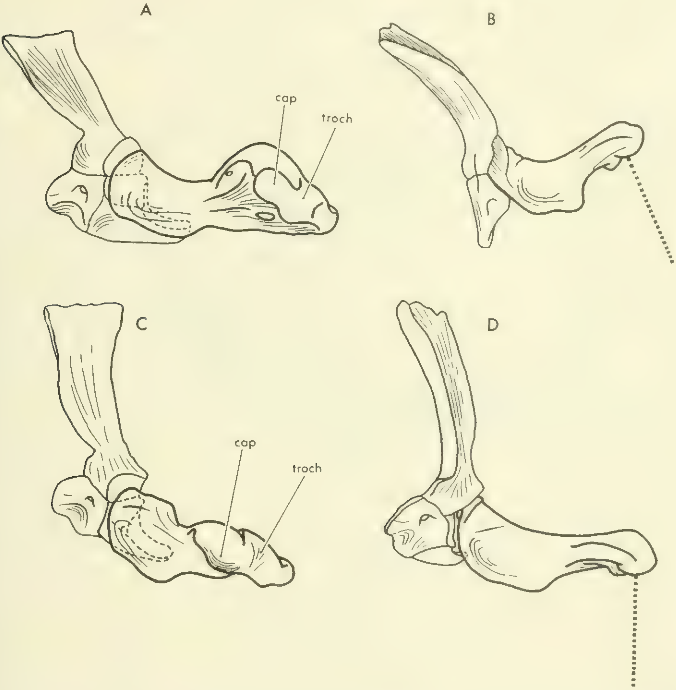

FIG. 40. A, lateral; B, anterior views of a cynodont scapulocoracoid and humerus to show the orientation of these bones as interpreted by Watson (1917a). C, lateral; D, anterior views of the same illustrating the present interpretation. *Dashed line*, antebrachial axis; *cap*, capitulum; *troch*, trochlea.

trally, the proximal end of the humerus rises dorsally to meet the glenoid and the distal end is depressed slightly below the glenoid level. The bowed relationship of the proximal and distal ends of the humerus further requires that the ventral edge of the coracoid plate be directed somewhat medially. If the coracoid plate is oriented vertically, as permitted by Watson (Fig. 40B), the humerus must orient in the glenoid in such a way that the capitulum and ventral part of the trochlea face ventrolaterally (Fig. 40A) instead of ventrally as required by a normal relationship with the antebrachium (Fig. 40D).

Correcting the foregoing inconsistencies in Watson's orientation of the scapulocoracoid and humerus a more realistic interpretation may be summarized as follows: lateral aspect of coracoid plate facing ventrolaterally as well as slightly anteriorly to conform with thoracic curvature; scapular blade inclining approximately 25° ante-

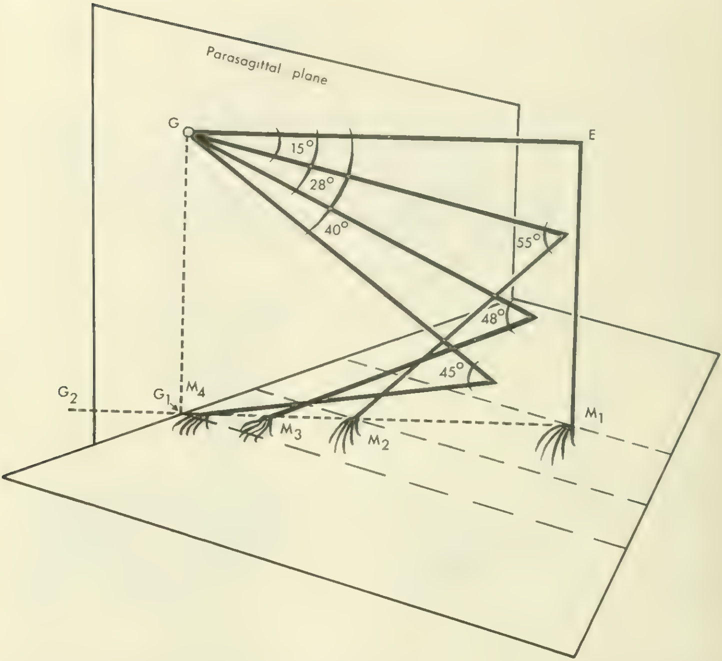

FIG. 41. Diagrammatic representation of the mechanics of cynodont forelimb movement which follows from Watson's (1917a) interpretation. Watson believed that the cynodont forelimb moved primarily in a plane (G, E, M_1, G_1) at 45° to a parasagittal plane as here represented. See text for further explanation.

riorly; glenoid facing posterolaterally as well as slightly ventrally; long axis of humerus at an angle of 45° to sagittal plane; distal end of the humerus somewhat lower than the glenoid and with the capitular surface directed more or less ventrally.

Gregory and Camp (1918) were the first to make direct comparisons between the cynodont and monotreme shoulder girdle and humerus; their restoration of *Cynognathus* forelimb and shoulder musculature implied that cynodonts had achieved a basically "prototherian" grade of organization in this respect. Yet these authors explicitly stated that the shoulder girdle in *Cynognathus* is "almost intermediate between *Sphenodon* and monotremes" insofar as both primitive reptilian and mammalian features are represented. Nevertheless the numerous, and rather superficial, points of comparison that Gregory and Camp drew between the shoulder girdle in monotremes and cynodonts invites the conclusion that monotreme anatomy represents a primitive structural stage of mammalian evolution toward which cynodonts were progressing.

Certainly the cynodont shoulder girdle already possessed certain features which monotremes retain, e.g., the eversion of the cranial border, or scapular spine, and morphology and orientation of the coracoids. However it is more accurate to classify these features as pertaining to a cynodont rather than a prototherian level of organization because monotremes have evolved distinct postcranial specializations of their own. These specializations, primarily associated with a fossorial habitus, invalidate the assumption that monotremes represent a general prototype of primitive mammalian structure and function. Howell (1936: 425) wrote that "with few exceptions (as Ribbing) most of those who have worked with monotremes have implied that they are among the most primitive mammals in their myological arrangement, as well as in general features. On the contrary, their musculature is so extremely specialized that it is very misleading to use this order for illustrating early steps in the phylogeny of mammalian myology." Howell's opinion is perhaps as extreme as the view that he rejects. The truth of the matter lies in between, namely, that features of the monotreme postcranial musculoskeletal anatomy must be evaluated individually, for some are recognizable correlates of a fossorial habitus while others reflect a primitive heritage.

Glenoid orientation and humeral position are among the most obvious features in monotremes which might be compared with cynodonts. Superficially, at least, the rounded notch of the monotreme glenoid resembles the cynodont glenoid cavity; both are formed by the scapula and coracoid, a small part of the procoracoid contributing in cynodonts. The humeri of both show many morphological similarities. However certain important details of this comparison reveal that there are basic differences in the orientation of the glenoid and humerus. First, there are significant differences in the orientation of the glenoid within the Monotremata. In *Tachyglossus* the glenoid faces laterally and somewhat ventrally, whereas in *Ornithorhynchus* it faces posterolaterally and somewhat dorsally. If monotremes are primitive, which is the primitive orientation? In cynodonts, of course, the glenoid is interpreted as having faced posterolaterally and ventrally, an orientation not apparently represented among monotremes. As for the position of the humerus, an examination of monotreme skeletal material, both articulated and disarticulated specimens, shows that the distal end of the humerus is held at a higher level than the proximal end—a feature developed in parallel among the fossorial Insectivora. Correlated with this is a typically long antebrachium which is, in *Tachyglossus* and *Ornithorhynchus* at least, 100 percent or slightly more of the humeral length. A relatively elongate antebrachium is perhaps a response to the height lost due to the repositioning of the humerus subsequent to fossorial adaptation. Some of the reasons why such a posture was probably not characteristic of cynodonts are discussed above with reference to Watson's (1917a) paper. The distal end of the cynodont humerus appears to have been normally positioned below the level of the glenoid, a fact clearly depicted by Gregory and Camp's (1918: Pl. XLI) comparative illustration of *Cynognathus* and *Ornithorhynchus*. Furthermore, the cynodont antebrachium is known to be on the order of only 75 percent of the humeral length (see below). If the cynodont humerus assumed a monotreme posture the forelimb would not be long enough to maintain the trunk well off the ground during locomotion.

Monotremes do not appear to represent a reliable model on which to base interpretations of the cynodont glenoid and humeral orientation. Further functional and comparative anatomical studies on the Prototheria may provide a sound basis for discriminating habitus from heritage features in these and other characters. At the present time, however, one must regard the cynodont, not the monotreme, as representing the primitive, "prototherian" pattern.

Locomotion

Watson (1917a: 29–30) made deductions concerning the locomotory function of the cynodont forelimb. He believed that excursion of the humerus was limited to depression and elevation along a vertical track, with no anteroposterior movement of the distal end. The forefoot is placed on the ground ahead of and medial to the glenoid by fully depressing the humerus. From such a position the humerus is elevated and the antebrachium extended, driving the glenoid over the forefoot. At this stage the antebrachium continues extension but the humerus is depressed, thus moving the glenoid in front of the forefoot to complete the stroke. In this interpretation Watson overlooked several important anatomical features and also apparently was not aware of some awkward biomechanical implications that his theory of forelimb function entailed. First, Watson admitted to not having seen any cynodont radius or ulna; these are now known from an associated skeleton of *Diademodon* sp. (USNM 23352) to be on the order of 75 per cent of humeral length. The relative shortness of the antebrachium, therefore, makes it improbable that the foot could have been placed much in advance of the glenoid in the manner Watson proposed. In Figure 41 the forelimb of *Diademodon* is drawn diagrammatically to scale. The view is perpendicular to a plane with corners at the glenoid (G), the elbow joint (E), the manus (M_1), and a point below the glenoid (G_1). Watson claimed that the forelimb must act along this plane which lies at 45° to the sagittal plane. In his view the manus must fall at some point along the line M_1-G_2. In order for the manus to reach a point just short of the glenoid (M_4) the humerus must depress 40° and the antebrachium must be flexed on the humerus at least 45°. However the articular facets involved do not permit this much depression or flexion. The abrupt ventral termination of the humeral head by the bicipital groove leaves little or no facet surface to contact the glenoid when the humerus is depressed by 40°. It is even less likely that the antebrachium could have been flexed within 45° of the humerus since no part of the trochlea or capitulum faces sufficiently proximally. In order for the manus to reach a point (G_2) beyond the glenoid, which Watson claimed was the case for cynodonts and probably occurs in all tetrapods, the amount of flexion and humeral depression reaches impossible limits.

Another factor that casts doubt on Watson's interpretation is the amount of lateral movement that would be generated. At each stride, no matter what the length, the shoulder girdle, and consequently the body, would be moved as much toward the contralateral side as forward. The greater the stride along the line M_1-G_1 the more the body is displaced contralaterally during the propulsive phase. Such a locomotory mechanism would be extremely clumsy and strenuous and has no analogy among any living or fossil tetrapod. If the stride is shortened to M_3, for instance, excessive flexion of the forearm is still required and the contralateral displacement is almost as great as for M_4. At position M_2 the degree of depression and flexion are within possible limits but the stride length is shortened to about one-half the humeral length—extremely inefficient and unlikely for the predaceous animals that some cynodonts were.

Watson (1917a: 27) claimed that "the cylindrical shape of the humeral articulation shows that the bone can have had freedom of motion only in the vertical plane". Cylindrical is an apt but incomplete description of the cynodont humeral head in which maximum curvature is dorsoventral. Depending upon the preservation there is also mediolateral curvature (Fig. 27A), and thereby the head approximates the spherical condition of mammalian humeral heads. The cynodont glenoid does not closely match the form of the humeral head (cf. Figs. 21 and 27A) although the articular cartilage probably formed somewhat more congruent surfaces. The scapular and coracoid halves of the glenoid are not smoothly confluent to form a cylindrical cavity but have an angular contact along the scapulocoracoid joint. The glenoid is therefore notch-like (Fig. 21). This distinct angulation gives the appearance of functionally discrete surfaces, a possibility that will be discussed below. Contrary to Watson's claim both the scapular and coracoid surfaces of the glenoid are not flat, for the latter in particular shows anteroposterior curvature. Moreover, the anterolateral (or external) margin of the glenoid consistently extends so far anteriorly in relation to the rest of the margin that the glenoid outline is asymmetrical; the most anterior part of the glenoid faces directly laterally in contrast to the remainder of the cavity which is oriented posterolaterally (Fig. 21). The glenoid is therefore not a close fitting counterpart to the humeral head but bears irregularities which must be interpreted in terms of greater freedom of humeral movement than Watson allowed.

The following interpretation of cynodont forelimb mechanics takes into account the range of movements which appear morphologically possible and which relate to the basic pattern developed among earlier synapsids. Pelycosaur humeri swung anteroposteriorly, but in doing so were adducted (depressed) or abducted (elevated) and rotated along their long axes. It is very likely that cynodont humeri had a similar pattern of movement because osteologically and therefore presumably myologically (as will be shown below) they are not far removed from the pelycosaur condition. However, unlike that in pelycosaurs the cynodont glenohumeral articulation does not restrict humeral positions. The recovery stroke probably involved abduction (elevation) of the humerus, as it does in most tetrapods, as well as anterior movement and longitudinal rotation of the humerus. The glenohumeral articulation obviously permits abduction, as Watson noted, and the anterolateral extension of the glenoid allows the humerus to swing anteriorly. There is no direct evidence for longitudinal rotation of the humerus, although a rotation of about 30° appears theoretically possible for this joint type. However in view of the increase in stride distance made possible by humeral rotation it is likely that the cynodonts, like their pelycosaur ancestors, preserved this functionally advantageous component in forelimb movement. As the humerus is brought forward and rotated clockwise (Fig. 42A–C) the lesser tuberosity tends to contact the posteromedial surface of the coracoid half of the glenoid; the slight recess (*Rec*, Fig. 21) in the glenoid surface at this point may have accommodated the incursion of this structure.

During the propulsive phase (Fig. 42D,E) the humerus is retracted posteriorly with respect to the glenoid and at the same time is depressed and rotated. The rota-

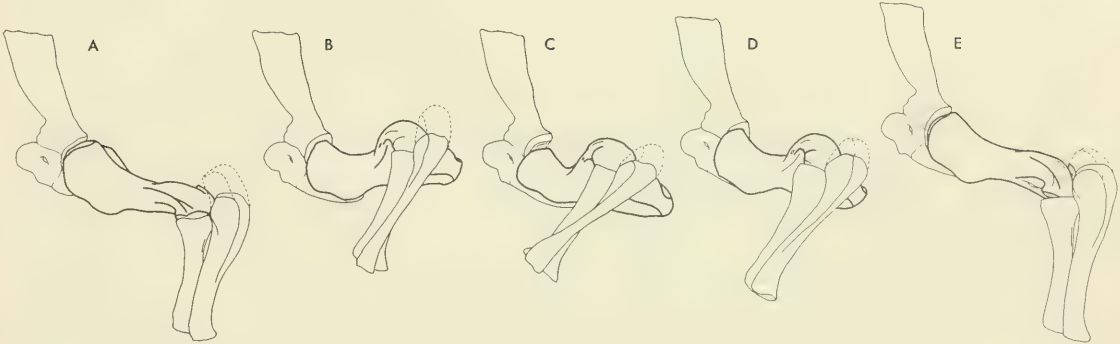

FIG. 42. Interpretation of the movement of a cynodont forelimb during locomotion, as seen in lateral view. A, stationary position; B, initial forward movement of limb: humerus elevated and rotated (clockwise on left side), antebrachium flexed; C, forelimb positioned for initial propulsion: humerus depressed, rotation continued from B, maximum antebrachial flexion; D, propulsive phase: humerus depressed and rotated (counterclockwise on left side), antebrachium extending; E, completion of propulsive phase: humerus maximally depressed, rotation completed, antebrachium extended.

tion permits the antebrachium which is anteroventrally directed at the beginning of the stroke to be elevated vertically and thus drive the humerus forward. The antebrachium which is probably flexed during recovery is extended on the humerus during the propulsive phase.

The angular relationship of the coracoid and scapular halves of the glenoid cited above as possible evidence for a functional division in the glenoid may be analyzed in terms of recovery and propulsive phases in forelimb movement. In the recovery phase the distal end of the humerus is elevated (Fig. 42A–C); simultaneously the head is depressed and contacts the lower (coracoid) half of the glenoid (*a*, Fig. 21). This surface is convex but slopes primarily anteroventrally. The humeral head, also being convex, makes minimal contact (which reduces friction) and is easily moved anteroventrally (*b*, Fig. 21). In this position both proximal and distal ends of the humerus are anteriorly situated for the beginning of the propulsive stroke (Fig. 42C). As the distal end of the humerus is depressed at the beginning of the propulsive phase (Fig. 42D) the head is raised and gains contact with the scapular half of the glenoid (*c*, Fig. 21). This half of the glenoid, facing posteroventrally and somewhat laterally, receives the thrust of the propulsive stroke which is directed anterodorsally and somewhat medially. The glenoid arrangement in cynodonts is therefore analogous to that in pelycosaurs with the anterior or scapular glenoid receiving the propulsive thrust and the posterior or coracoid glenoid elevating the humerus in the recovery phase. The scapular glenoid is stoutly built around the base of the scapular blade to withstand propulsive stress and to transmit body weight to the humerus.

From the position illustrated in Figure 42C, the propulsive stroke is completed by extension of the elbow joint coupled with a slight counter-clockwise (seen from the left) rotation of the humerus (Fig. 42D,E). These actions elevate the body and move it forward.

In terms of forelimb movements cynodonts probably did not depart from the basic pelycosaurian locomotory pattern although loss of the screw-shaped glenoid permitted greater freedom of movement. However, the orientation and relationship of cynodont shoulder girdle and limb elements are so much modified that despite a primitive pattern of limb movement the resulting mechanical system is well advanced toward a mammalian condition. The following are major functional differences between pelycosaurs and cynodonts with regard to the forelimb and girdle:

1) In cynodonts the glenoid is formed by contributions from the scapula, coracoid and procoracoid as in pelycosaurs, but the procoracoid contribution is extremely small. The monotreme procoracoid is excluded from the glenoid. In terms of the composition of the glenoid, pelycosaurs, cynodonts and monotremes form a morphogenic series. However the monotreme glenoid is otherwise quite specialized in orientation (see above) and morphology. Shaped as a crescentic, symmetric notch, the monotreme glenoid is of a pattern similar to that found among modern lacertilians. In cross-section the glenoid is C-shaped with dorsal and ventral aspects of the cavity smoothly confluent. In cynodonts the glenoid is asymmetric, the largest part being borne by the scapula. The asymmetry is in part related to differentiation of discrete functional areas of the glenoid (see above), a trend already begun in pelycosaurs and in other primitive tetrapods. Functional differentiation of the cynodont glenoid especially with

regard to the nearly circular and slightly concave scapular part presages the development of the mammalian scapular glenoid.

2) In cynodonts the scapular glenoid which receives the propulsive thrust faces posteroventrally and slightly laterally whereas in pelycosaurs the analogous surface faces posterolaterally and very slightly, if at all, ventrally. The obvious difference in cynodonts is the reduction of the lateral component in propulsion which does not contribute to forward locomotion.

3) As a corollary to (2) the component of forward thrust in cynodonts is more closely aligned with the long axis of the scapular blade than it is in pelycosaurs. Since the resistance to forward thrust, in terms of body weight, is in large part transmitted via the scapula, propulsive forces which do not act in close opposition to the main axis of the scapula tend to produce torque. Among pelycosaurs the gravitational force of body weight borne by the scapula passes in a ventral direction through the glenoid but the force due to propulsive thrust passes anteromedially through the glenoid; the resulting torque tends to rotate the anterior border of scapulocoracoid medially. This torque is obviously resisted by the robust clavicles and interclavicle. In cynodonts the propulsive thrust is against the scapular base and is directed anterodorsally and only slightly medially. The direction of such force accounts for the anterior inclination as well as the medial curvature of the scapular blade which is reoriented so that both gravitational and propulsive forces are transmitted more in line with its own axis. This represents an initial stage in the trend toward a mammalian scapula which alone (or with a much reduced clavicle) transmits forces between body and humerus.

4) In pelycosaurs the long axis of the humerus, from head to trochlea, is straight and in average position is horizontal. In cynodonts the proximal half of the long axis is bowed ventrally so that in average position the humerus is depressed below the glenoid level. A less horizontally oriented humerus is an important stage in the reduction of medially directed forces which necessitate the primitive, "braced" type of shoulder girdle. A more vertically oriented humerus transmits proportionally greater propulsive forces directly to the scapula.

5) The inferred arrangement of scapulocoracoid musculature in cynodonts, although scarcely mammalian in plan, represents an advanced stage in an evolutionary trend established in the stegocephalian-cotylosaurian-pelycosaurian grades. The importance of medial curvature in the scapular blade to the reorientation of serratus musculature has been shown above (see p. 135); by reducing the role of the pectoral girdle in resisting compressive (transverse) forces the pectoral girdle loses its structural massiveness and gains the potential of participating in forelimb movement as in mammals. Other apparent trends in muscular displacement relate primarily to the origins of humeral rotators which appear to have become arranged for more efficient and perhaps rapid rotation. In addition the tendency to increase the area of attachment of humeral adductor muscles is evidence that these may have increased in size, functional importance or both.

In primitive tetrapods the M. subcoracoscapularis, originating on the dorsomedial

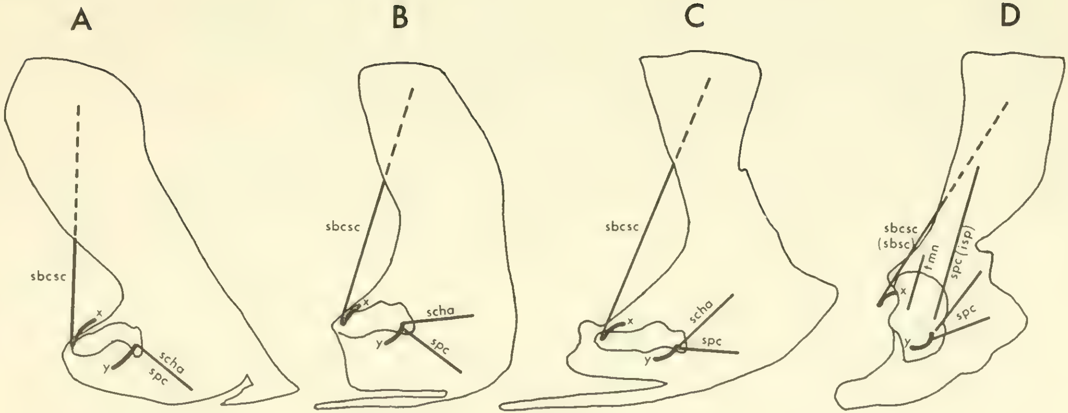
A
B
C
D
sbcsc
x
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FIG. 43. Diagrammatic representations of the scapulocoracoid plate and reconstructed muscle actions in A, *Eryops; B, Diadectes; C, Dimetrodon; D, Cynognathus. x,* position of the insertion of subcoracoscapularis musculature at the completion of the propulsive phase; *y,* the same for supracoracoideus musculature. Other abbreviations as in FIG. 19.

surface of the scapula and inserting on the proximointernal angle of the humerus, analogous to a lesser tuberosity, elevated the posteror aspect of the humerus. This movement, assisted by the guiding "trackway" of the screw-shaped glenoid, brought about an anteroventral rotation of the humerus during the propulsive stroke. In *Eryops* (Fig. 43A) the traction of the subcoracoscapularis is directly dorsal or perhaps slightly posterodorsal. The arc of movement described by the point of insertion is a segment of a relatively large circle, and thus the total longitudinal rotation of the humerus is small per unit of muscular contraction. In *Diadectes* and *Dimetrodon* (Fig. 43B,C) the scapular blade is displaced anteriorly relative to the glenoid and so also is the origin of the subcoracoscapularis relative to its insertion. The inferred traction is anterodorsally directed, slightly more in *Dimetrodon* than in *Diadectes*, and thus rotation of the point of insertion (to x) is greater per unit of muscular contraction. In other words, the arc described by the rotation of the subcoracoscapularis insertion is a segment of a relatively smaller circle than in *Eryops*, with the consequent possibility of more rapid movement. In cynodonts (Fig. 43D) this trend is carried still further. The foregoing analysis is not an estimate of the amount of anteroventral rotation but only the relative efficiency with which this rotation was accomplished. In *Eryops* longitudinal rotation was perhaps as much as 90° (Miner, 1925: 167) but in cynodonts it could not have been more than 30°.

The Mm. scapulohumeralis anterior and supracoracoideus of primitive tetrapods opposed the subcoracoscapularis by effecting reverse rotation as the humerus was brought forward during the recovery stroke. In *Eryops* (Fig. 43A) these muscles probably took origin ventrally on the procoracoid in a position anteroventral to their insertion on the proximoexternal angle of the humerus (analogous to a greater tuberosity). When the humerus had completed the anteroventral rotation of the propulsive stroke these muscles effected a posterodorsal counter-rotation starting from point y. This rotation took place along a broad arc which is a segment of a relatively large circle. In *Diadectes* and *Dimetrodon* (Fig. 43B,C) the origins of these muscles were probably displaced dorsally thereby bringing the line of traction more directly in line with the path of the point of insertion. The mechanical advantage gained by this arrangement is further developed in the cynodonts in which the supracoracoideus is positioned to rotate its point of insertion almost directly dorsally (Fig. 43D).

The history of the coracoid head of the triceps relates to its function as an extensor of the antebrachium and in more advanced forms as a retractor of the humerus. In *Diadectes* (and presumably in *Eryops*; Fig. 19A,B), it took origin immediately posterior to the glenoid and probably functioned only as an antebrachial extensor (Romer, 1922b: 537). In *Dimetrodon* (Fig. 19C) its origin is displaced sufficiently posterior to the glenoid that the olecranon would not only be pulled medially, hence antebrachial extension, but also posteriorly, thus effecting humeral retraction. In cynodonts this condition is accentuated, imparting a true posterior component to its traction. This condition is necessitated by the shift in glenoid orientation to a more posterior-facing position which would mask the origin of the coracoid triceps if it were not also displaced posteriorly. A coracoid head of the triceps is lacking in monotremes (McKay, 1894) as it is in other mammals. Superficially, at least, the posteriorly reflected coracoid process of monotremes is similar to that of cynodonts (Fig. 19F,G). In monotremes the coracobrachialis and a biceps head take origin from its apex (Westling, 1889 and Howell, 1937a) whereas in cynodonts it is here claimed that the coracoid head of the triceps arose from the apparently analogous position. However, a strong possibility exists that the monotreme pattern is indeed a primitive mammalian arrangement, and that the so-called coracoid process for the triceps in cynodonts bore the coracobrachialis and the short head of the biceps. In this case the coracoid triceps head would already have been lost. This problem cannot be solved without additional material demonstrating a more complete range of intermediate stages. At present there are so many known specializations in monotreme myology that no aspect of their locomotory anatomy can be assumed to be primitive prima facie.

The relative increase in size of the interclavicle undoubtedly correlates with the functional importance of the M. pectoralis. In *Eryops* (Fig. 19A) the interclavicle is a small plate anteroventral to the glenoid. It seems unlikely that pectoral musculature from such an origin alone could have effected the strong humeral adduction which is necessary in part to raise the body off the ground. Romer (1922b: 528) suggested that primitively the pectoralis took origin also from the sternum and surface of the M. rectus. In *Diadectes* and *Dimetrodon* as well as in *Sphenodon* and *Iguana* (Fig. 19B E) pectoral musculature has extensive origin from an elongate interclavicle, evidence of powerful adduction and an increased ability to sustain the body above the ground. In cynodonts the interclavicle was proportionately as long as that in pelycosaurs and relatively wider. The deltopectoral crest (on which the M. pectoralis inserts) increased in relative length; in a typical specimen of *Dimetrodon* (MCZ 3357) the length of the crest is 36 percent of humeral length while in cynodonts it is commonly 50 to 55 percent or more. Some rather specialized cynodonts possessed a deep, ventral keel on the interclavicle that would appear to be direct evidence of a well-developed pectoralis. In African cynodonts an interclavicular keel was not an osseous structure but may have been present in cartilage. I conclude that cynodonts had increased power of humeral adduction and that the posterior extension of the interclavicle permitted more effective humeral retraction during the propulsive stroke.

The phylogenetic displacement of shoulder musculature leading to the cynodont arrangement increased the efficiency and power of locomotory movements already developed among earlier tetrapods: humeral rotation (subcoracoideus, scapulohumeralis anterior and subcoracoscapularis), humeral retraction (pectoralis, coracoid triceps), and humeral adduction (pectoralis). These changes are largely an improvement of a primitive system rather than innovation. Yet the position of the humerus and the orientation of the glenoid are substantially advanced toward a mammalian condition. It cannot be maintained that the cynodont shoulder girdle and forelimb were "primitive" or "reptilian"—any more than it can be maintained that they achieved a typically mammalian grade of organization.

PART THREE. APPENDICULAR SKELETON: PELVIS AND HINDLIMB

1. PELVIS (Figs. 44-47)

MATERIAL. The pelvis of *Cynognathus crateronotus* (BMNH R.2571; see Seeley, 1895b: 112-119) is one of the most complete cynodont pelves known to date. The iliac blade is missing from the left side and is only partially preserved on the right. Plaster has been utilized to rejoin the separate pieces particularly around the acetabulum and therefore the specimen is of little use in determining the nature of the hip joint. Otherwise this pelvis displays many features not preserved in any other specimen, notably the ventral junction between the two ischia and pubes.

The pelvis in *Thrinaxodon* is known adequately from a large number of specimens. The most useful is AMMM 5265 which preserves both ilia and the sacroiliac synchondrosis although the pubes and ischia are disarticulated and damaged. Numerous other specimens (AMNH 2228, BPI 287, NMB C.143, NMB C.318, NMB C.392 and SAM K.1395) provide additional material in various states of preservation and preparation.

An excellently-preserved right half of a pelvis is known in a Middle Triassic cynodont (BMNH TR.8) from the Manda Formation of Tanzania. The cranial fragments associated with this material are generically indeterminate, but may represent either *Scalenodon* or *Aleodon* (A. W. Crompton, pers. comm.). This cynodont possessed lumbar ribs of the *Cynognathus-Diademodon* type. The specimen is particularly important because the acetabulum is well preserved and is associated with a complete femur. Also from the Manda is a disassociated pubis of a generically indeterminate cynodont about twice the size of BMNH TR.8 (von Huene, 1950).

Broom (1905a: 99-100) described the ilium, ischium and pubis of *Diademodon mastacus*, but the specimen is not housed in any museum and is apparently lost. His incomplete account agrees in most details with the pelvic elements of *Diademodon* and *Cynognathus* described here from other sources.

Disarticulated ilia and ischia of *Cynognathus* and *Diademodon* are preserved in one collection (NMB C.2099; NMB C.2702), but generic separation of the individual bones is not possible. Another similar collection (BPI 1675) provides fragmentary pubes as well as ilia and ischia of these genera.

Haughton (1924: 89) described an ischium (TM 83) associated with *Glochinodontoides gracilis*; comparison with *Thrinaxodon* shows no substantial difference other than a larger size.

In the D.M.S. Watson Collection, there are a number of cynodont pelvic fragments, most of them generically indeterminate but very similar to the *Cynognathus-Diademodon* pattern. The most complete is DMSW R.225, a right half of a pelvis lacking only part of the iliac blade. In this specimen the suture between ilium, ischium and pubis is fused, retaining the three bones in their correct relative positions. Brink's (1955) description of the pelvis in *Diademodon* is apparently based on material in the D.M.S. Watson collection.

Broom (1932b: 239) claimed that in *Galesaurus* "the ilium is somewhat similar to that in *Thrinaxodon*, but more rounded and considerably higher". Since Broom's specimen is neither figured nor cited, the comparison is of doubtful significance—especially considering the inaccuracy of Broom's (1932b: fig. 91) figure of the ilium and pubis in *Thrinaxodon*. Parrington (1934) described the pelvis of *Galesaurus* from a specimen (UMC R.2722) which cannot be referred with certainty to this genus (see p. 62). Nevertheless, the specimen is undoubtedly galesaurid and morphologically is indistinguishable from *Thrinaxodon*.

A complete although disarticulated pelvis of *Leavachia duvenhagei* (RC 92; Broom, 1948: 626–627) is rather similar to other cynodont pelves except that the iliac blade has only a small posterior extension; this feature in contrast to other African cynodonts is similar to that developed in the South American traversodontid *Exaeretodon* (Bonaparte, 1963a; see discussion in Jenkins, 1970a).

Ilium

MORPHOLOGY. The cynodont ilium is composed of a thin, moderately expanded iliac blade separated from a base by a constricted neck (Fig. 44). The base bears a third of the acetabulum and facets for contact with the pubis and ischium. Anteriorly the blade outline in *Thrinaxodon*, *Cynognathus* and *Diademodon* is broadly rounded and somewhat spoon-shaped. Posteriorly the outline is angular with the straight posteroventral edge of the blade intersecting the gently convex dorsal (vertebral) edge at an angle of approximately 80°. The exact outline of the blade varies with ossification. In *Thrinaxodon* the dorsal edge often appears less convex than in larger cynodonts, imparting a lanceolate outline to the posterior terminus of the blade. The straight, evenly sloping dorsal edge of the *Diademodon* ilium figured by Broom (1905: Pl. I) undoubtedly represents an incomplete specimen. Brink (1955) also claimed that the upper (vertebral) margin of the ilium is perfectly straight; such a condition would approximate the morphology typical of primitive mammals. Brink's observation may have been based on DMSW R.225 in which the ilium appears to be straight. The iliac blade of this specimen is almost certainly incomplete and more complete specimens have an outline such as illustrated in Figure 44.

The anterior and dorsal edges of the iliac blade abruptly attenuate to a sharp rim; the rugosity of the rim is evidence of a cartilaginous supra-iliac blade. The deepest (highest) section of the blade often lies directly above the most anterior part of the acetabulum but marginal damage to all specimens leaves the true outline in doubt. The blade is uniformly rather thin except at the base, where the supra-acetabular buttress (*spa bu*, Fig. 44) contributes to the thickness, and along the straight posteroven-

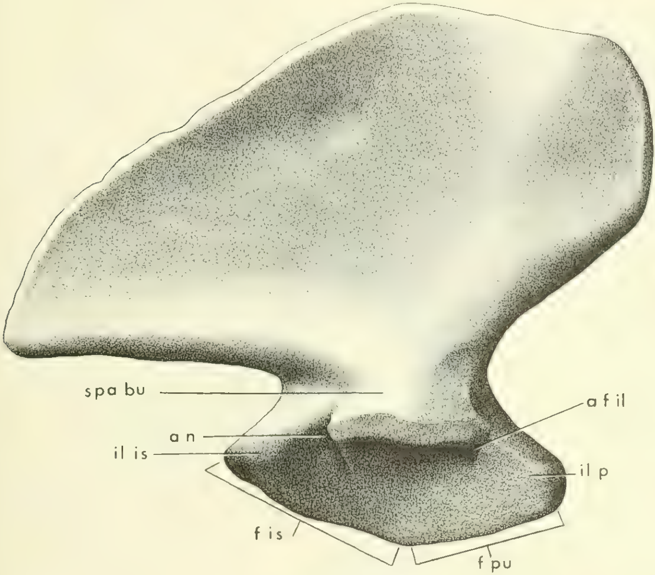

FIG. 44. Right ilium of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, in lateral view. The small, round depression in the center of the blade is probably the result of post-mortem damage, and perhaps represents a tooth mark. X1. Abbreviations: *a f il,* acetabular facet of the ilium; *a n,* acetabular notch; *f is,* facet for articulation with the ischium; *f pu,* facet for articulation with the pubis; *il is,* ischial process of the ilium; *il p,* pubic process of the ilium; *spa bu,* supra-acetabular buttress.

tral edge which is swollen into a rod-like buttress extending from the posterior end of the ilium to the supra-acetabular buttress. In *Diademodon*, *Cynognathus* and other cynodonts a slight thickening of the blade occurs in an area anterodorsal to the acetabulum. This thickening is manifested on the lateral surface of the iliac blade by a low, vertical ridge which thus delineates two shallow fossae of unequal size (Figs. 44, 46A); the anterior and smaller of the two fossae may represent some differentiation of the gluteal musculature, the mammalian homologue of the M. ilio-femoralis of reptiles. The bone surface texture of the entire lateral surface of the iliac blade is commonly smooth and devoid of muscle markings. In larger cynodonts the lateral surface may bear a small number of irregularly spaced striations radiating away from the neck (*st*, Fig. 45A). The medial surface of all cynodont ilia bears a pattern of striations radiating away from, but not quite reaching, the neck (*st*, Fig. 46B). Striations are most strongly developed on the anterior half of the blade where they may extend to the anterior and dorsal margin. The striations on the medial iliac surface record the presence of extensive connective tissue in the sacroiliac syndesmosis.

The base of the ilium is broad mediolaterally, consisting of a laterally projecting supra-acetabular buttress (*spa bu*, Fig. 44), an anteromedially directed process for articulation with the pubis (*il p*), and a posteromedially directed process for the ischium (*il is*). In many specimens the supra-acetabular buttress appears to be reflected somewhat dorsolaterally, and the pubic and ischial processes project ventrally and lie directly beneath the blade. This condition is unquestionably due to postmortem compression, for in the few relatively undistorted ilia (AMMM 5265, AMNH 2228, BMNH R.2571, NMB C.2699) the supra-acetabular buttress projects nearly as much laterally as do the pubic and ischial processes medially. The buttress is similarly developed in *Chiniquodon* (Romer, 1969a).

The iliac facet of the acetabulum is concave and faces for the most part directly ventrally (*a f il*, Figs. 44, 46A). The lateral rim of the facet is round; medially the anterior and posterior rims may converge and intersect at an 80° angle. In most specimens, however, the ossification is not sufficiently complete to distinguish the medial half of the facet from the lateral surfaces of the pubic and ischial processes and the facet appears to merge with these surfaces (Figs. 44, 46A).

Posterior to the supra-acetabular buttress is a deep recess, or so-called supra-acetabular notch (*a n*, Figs. 44, 46A, 50B). Broili (1908: 3–4) first called attention to this feature in dicynodonts, and noted its presence in *Cynognathus*. Romer (1922b: 581) concurred with Broili that it marked the position "of a ligament similar to that found in the cotyloid notch of the ischium of mammals". In mammals the homologous notch has shifted ventrally and, as Romer noted, the change in femoral position accounts for this displacement (*a n*, Fig. 50C). Two ligaments are associated with this notch in mammals: the transverse acetabular ligament and the ligament of the head of the femur (ligamentum capitis femoris). There is no direct evidence that cynodonts possessed a femoral head ligament. However, the acetabular notch of cynodonts was probably covered by a transverse acetabular ligament, thus creating a passageway for neurovascular structures supplying the femoral head and joint capsule.

The thickness of the pubic and ischial processes is approximately twice that of the iliac blade although the thickness is somewhat less along their juncture. The articular surfaces are strap-shaped, widening at the anterior (pubic) and posterior (ischial) ends (*f pu*, *f is*, Fig. 44). The pubic surface in well-preserved specimens is about three-quarters of the length of the ischial and faces more or less ventrally. The ischial surface faces posteroventrally and adjoins the pubic at an angle of from 130 to 150°.

PUBIS

MORPHOLOGY. The pubis consists of a dorsal head, bearing the acetabular facet and articular surfaces for pubis and ilium, and a ventromedially directed blade. The acetabular facet, which faces posterodorsally as well as laterally, may be oval (*a f pu*, Fig. 45A) or may represent only part of an oval (*a f pu*, Fig. 46A); in either case its long axis is oriented posteroventrally. During life the cartilaginous articular surface was probably concave. In area the pubic facet is the smallest of the three facets comprising the acetabulum. Moreover the lateral rim of the pubic facet does not

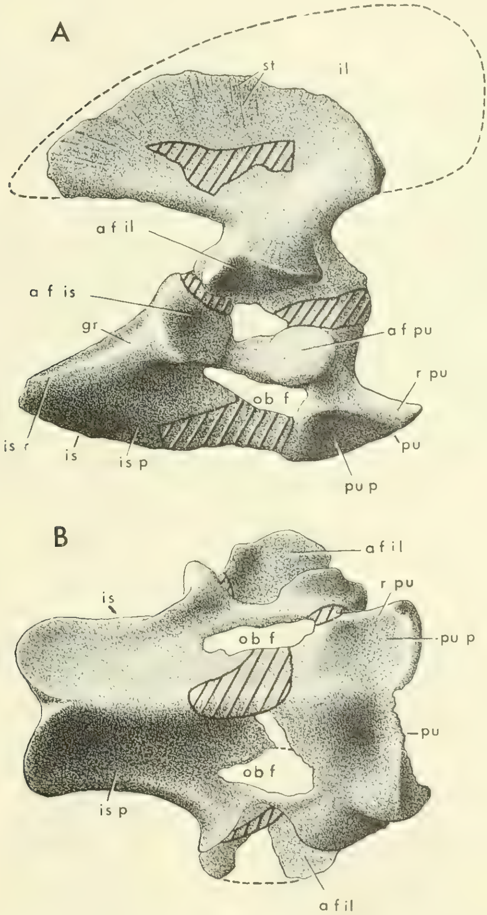
A
st
il
a f il
a f is
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FIG. 45. Pelvis of the type of *Cynognathus crateronotus*, BMNH R. 2571, in A, lateral; B, ventral views. Oblique hatching indicates plaster reconstruction. Matrix adheres to the anterior part of the left pubis in B and it therefore appears to be different from right pubis. X0.45. Abbreviations: *a f il*, acetabular facet of the ilium; *a f is*, acetabular facet of the ischium; *a f pu*, acetabular facet of the pubis; *gr*, groove in dorsal edge of ischium; *il*, ilium; *is*, *ischium*; *is p*, ischial plate; *is r*, ischial ridge; *ob f*, obturator foramen; *pu*, pubis; *pu p*, pubic plate; *r pu*, rod-like anterodorsal edge of pubis, *st*, iliac striations.

protrude as far laterally as the iliac and ischial facets (Fig. 46A and DMSW R.225). This feature which opens the acetabulum more anteriorly than posteriorly is important in the determination of femoral position (see below).

The dorsomedial rim of the head of the pubis is occupied by a rugose, strap-shaped surface which articulates with the pubic process of the ilium. At its posterior terminus the surface faces posteriorly and makes contact with the ischium above the obturator foramen. The anterior half of the strap-shaped surface gradually expands to a wide terminus which together with the expanded anterior edge of the pubic process of the ilium represents the strongest part of the iliopubic symphysis.

Below the head the pubis is constricted to form a short neck. From the neck arises a ventromedially directed pubic plate which is laterally concave (*pu p*, Fig. 45A). Most of the pubic plate is thin and in no specimen is it completely preserved. The plane of the pubic plate appears to be slightly convolute because its anterior edge arises from the anteromedial surface of the neck whereas the posterior edge arises from the posteromedial surface. The anterodorsal edge of the pubic plate is swollen and rod-like (*r pu*, Figs. 45A, 46A), a primitive feature found is sphenacodontid and other pelycosaurs. The rod is slightly curved, bending ventrolaterally toward its anterior end. It terminates in a round, flat rugosity which has generally been interpreted (see below) as an articular facet for a prepubic bone. Opposing pubic plates meet along a thin symphysis, creating a broad, U-shaped basin which is deepest posteriorly along the puboischial contact. In no pubis is the anterior free edge completely preserved; presumably it was very thin and perhaps extended by cartilage. The posterior half of

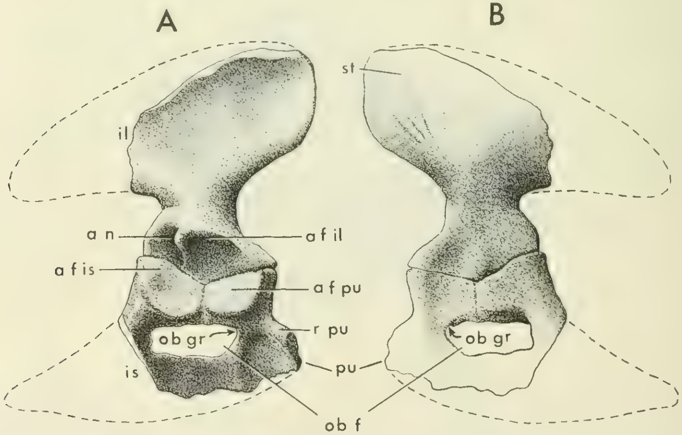


FIG. 46. Right side of the pelvis in a cynodont, BMNH TR.8, possibly referable to ?*Aleodon* or ?*Scalenodon*, in A, lateral; B, medial views. X1. Abbreviations as in FIG. 45 except: *a n*, acetabular notch; *ob gr*, groove across anterior edge of obturator foramen for the obturator nerve and vessels.

the pubic blade contacts the ilium beneath the obturator foramen. Spatulate in outline, this part of the blade is flat and of uniform thickness except along the obturator rim where it is slightly thickened.

Across the posterior edge of the neck of the pubis, which forms the anterior margin of the obturator foramen, runs a groove representing the course of the obturator nerve and vessels (*ob gr*, Fig. 46). The groove passes from the dorsomedial side of the neck to the ventrolateral side. This arrangement is essentially the same as in mammals.

The possibility of cynodont prepubic ("epipubic") bones has been suggested by many authors. Nineteenth century paleontologists (e.g., Owen, Seeley, etc.) often directly compared homologous bones in therapsids and marsupials and it is not surprising that the possibility of a prepubic ossification was introduced. Seeley (1895a: 40; 1895b: 116) stated that there is no evidence for an ossified prepubis in either *Microgomphodon* (=*Diademodon*) or *Cynognathus*. Nevertheless, later authors either restored a prepubis in cynodonts without elicting evidence (e.g., Gregory and Camp, 1918: Pl. XLIV; Goodrich, 1930: 200; Howell, 1944: fig. 21) or claimed that a cartilaginous or osseous prepubis is rendered probable by the flat rugosity (?"articular facet") at the terminus of the rod-like anterodorsal edge of the pubis (Romer, 1922b: 580; Gregory, 1947: 37). No cynodont prepubes have yet been discovered, and it seems unlikely, in view of Vaughn's (1956) work, that separate prepubic ossifications were present. Vaughn adduced evidence to show that the prepubic bones of monotremes and marsupials "represent a retention or replacement of a portion of the reptilian puboischiadic plate anterior to the lateral pubic tubercle [and] that this retention or replacement took place during the general posteriorward displacement of the pubis . . ." (ibid.: 260). The cynodont pubis which lacks the pubic tubercle has undergone only a relatively small amount of posterior displacement; the anterior margin of the pubis projects craniad well beyond the acetabulum. The impetus for the formation of separate prepubic ossification was therefore lacking. It is probable, however, that the rod-like anterodorsal edge was continued in cartilage as was the analogous feature in many pelycosaurs (Romer and Price, 1940: 132). Further posterior displacement of the pubis may well have necessitated the strengthening of this cartilage through ossification but apparently the cynodont pelvis is functionally too reptilian to require this mammalian development. It is interesting to note that among tritylodonts, which are advanced therapsids with a very mammal-like pelvis, prepubic bones are known (Fourie, 1962).

ISCHIUM

MORPHOLOGY. The ischium, like the pubis, is composed of a head and a ventromedially directed plate (*is p*, Fig. 47A,B). The head bears part of the acetabular surface for the femur as well as symphysial surfaces for the pubis and ilium. The acetabular facet of the ischium is approximately oval but its medial border (adjoining the ilium) is nearly straight (*a f is*, Fig. 46A). Ventrally the oval facet is narrower than dorsally and although poorly preserved in most specimens it was apparently concave during life. It faced anterolaterally and slightly dorsally (*a f is*, Fig. 46A; see also

DMSW R.225). The medial aspect of the ischial head bears a strap-shaped surface, which becomes broader dorsally, for articulation with the ischial process of the ilium (*f il*, Fig. 47B). This surface faces medially and dorsoanteriorly but at its cranial extremity it turns anteriorly to make a short contact with the pubis above the obturator foramen.

The neck between the ischial head and plate is short. A ridge extends from the middle of the lateral acetabular rim to the posterodorsal corner of the plate, gradually attenuating posteriorly (*is r*, Figs. 45A, 47A). At the posterodorsal corner it is terminated by a prominent but mediolaterally narrow ischial tuberosity (*is tb*, Fig. 47A C). The extent of the ridge and the development of the tuberosity is variable. In *Glochinodontoides gracilis* (TM 83) the ridge does not extend to the ischial tuberosity but joins the dorsal edge of the ischial plate midway between head and tuberosity. In *Thrinaxodon* the ridge may fade into the lateral surface of the plate before reaching the ischial tuberosity, which is relatively small, or may be represented only as a lateral thickening of the dorsal rim. Between the ridge and the dorsal edge of the plate is a shallow groove which faces posterolaterally (*gr*, Figs. 45A, 47A). The groove is well developed in *Cynognathus*, *Diademodon* and *Glochinodontoides* but in *Thrinaxodon* it is variable—incipiently developed in some specimens (BPI 3848), apparently absent in others where the ridge is least pronounced (AMMM 5265).

The rest of the ischial plate below the ridge and tuberosity is thin and elongate anteroposteriorly, more or less rectangular and slightly concave medially (Fig. 47A,B). An entire ischial plate has not yet been recovered although that of *Cynognathus crateronotus* (BMNH R.2571) is nearly complete and the outline may be confidently reconstructed from this and other specimens (NMB C.2702, DMSW R.225). The posterior edge of the plate is straight, passing medially and ventrally to form a broad, V-shaped notch with the corresponding edge of the other ischium. The ischial symphysis is long and narrow with the articular contact somewhat thicker anteriorly than posteriorly. The ischial symphysis is approximately twice as long as the pubic. Broom's (1905a: 100) claim that the ischial symphysis in *Diademodon* is shorter than in *Cynognathus* was based on a specimen in which the posteromedial corner was apparently missing. No evidence of a difference in ischial morphology between these genera exists in the Bloemfontein collection (NMB C.2702). The anterior part of the plate is a very thin flange which meets the posterior edge of the pubic plate beneath the obturator foramen. Most specimens are incomplete in this region, the exceptions being that figured by Broom (1905a: fig. 4), DMSW R.225, and BMNH TR.8.

The relative size and configuration of the obturator foramen in cynodonts other than *Cynognathus* and an unidentified Manda cynodont (BMNH TR.8) must remain in doubt until more complete pelves are known. Broom (1932b: 271, fig. 91) described and figured *Thrinaxodon* as having no obturator but only a small pubic foramen. Later Broom (1948: 626 627) reiterated his belief by remarking that "in the only nearly perfect pelvis of *Thrinaxodon* which I have been able to examine, the pubes and ischia are imperfectly co-ossified, and in life probably a thin strip of cartilage separates the bones". The *Thrinaxodon* pelvis alluded to in Broom's (1932b, 1948) papers is, like so many of his other specimens, apparently lost. It appears that Broom's claim was based upon a poorly ossified or possibly damaged specimen. The pubes and ischia of known specimens of *Thrinaxodon* (AMMM 5265, BPI 3848),

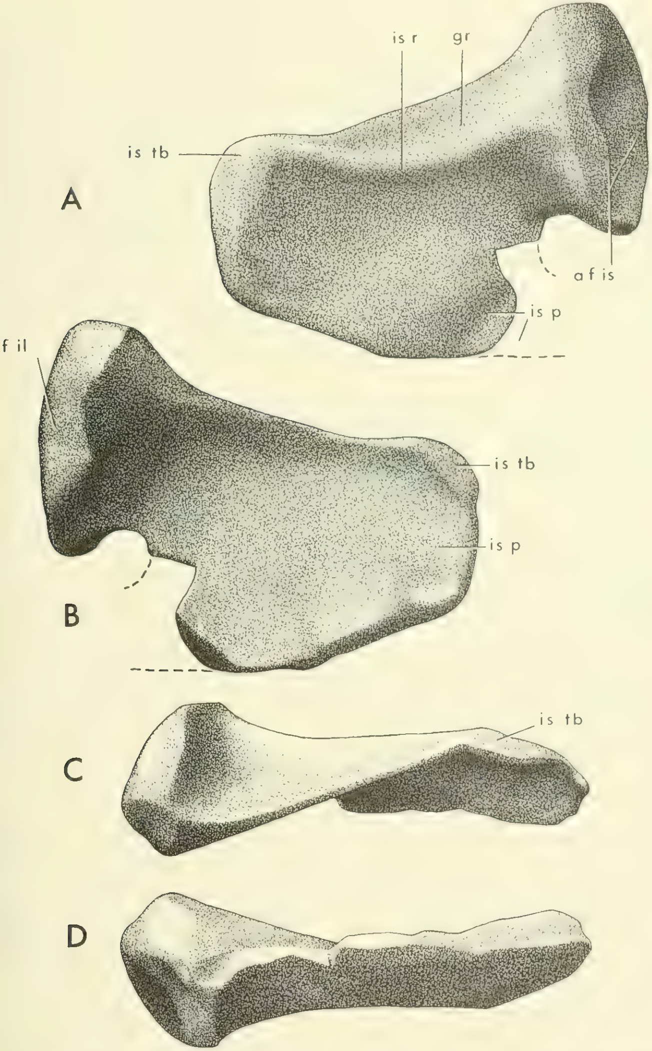

is r
gr
is tb
A
a f is
is p
f il
is tb
is p
B
is tb
C
D

FIG. 47. Right ischium of cf. ?*Cynognathus* (?*Diademodon*) NMB C.2702 in A, lateral; B, medial; C, dorsal; D, ventral views. X1. Abbreviations as in FIG. 45. except: *f il*, facet for articulation with the ilium; *is tb*, ischial tuberosity.

although disarticulated, show clearly the characteristic indentations for the obturator rim, and therefore *Thrinaxodon* possesses an obturator foramen as do all other cynodonts for which the pelvis is known. In *C. crateronotus* (BMNH R.2571) the large, oblong foramen is two-thirds as long as the acetabulum (*ob f*, Fig. 45). In this specimen the anterior (pubic) rim appears to be somewhat more broadly rounded than the posterior (ischial) rim but in fact the anterior rim is not well preserved. Other pubes of *Cynognathus* or *Diademodon* (BPI 1675; both genera are most certainly represented in this collection but no differences in the pubes are apparent) show only the characteristic oblique cleft or obturator groove passing laterally and posteroventrally across the anterior part of the obturator rim. In the unidentified Manda cynodont (BMNH TR.8) the obturator foramen is more or less square with rounded corners and in this respect approximates the foramen shape typical of mammals. In Figure 46 the foramen appears to be rectangular; this is due to the two dimensional representation of the puboischiadic plate which is reflected medially.

2. HINDLIMB

FEMUR (Figs. 48, 49)

MATERIAL. Cynodont femora are adequately known in *Thrinaxodon* (SAM K. 1395; BPI 287, BPI 376; NMB 392) and in two collections in which disarticulated skeletons of *Cynognathus* and *Diademodon* are intermixed (BPI 1675, NMB C.2694). Except for differences of size and variations in ossification the femoral morphology is essentially the same for all three genera.

The proximal half of the femur associated with the type of *Cynognathus crateronotus* (BMNH R.2571) is poorly preserved. This fact accounts for various misconceptions, usually concerning the cynodont femoral head and trochanters, which are based on this one inadequate specimen.

The one known femur of *Glochinodontoides gracilis* (TM 83), described by Haughton (1924: 88–89), is only partially prepared but shows no significant differences from the above genera.

A large cynodont femur (SAM 977) in the South African Museum is identified as belonging to *Gomphognathus kannemeyeri*, one of the genera synonomized with *Diademodon* by Watson and Romer (1956: 65). In view of the lack of associated diagnostic cranial material (only a tibia is preserved with this specimen) this specimen is generically indeterminate and could represent either *Cynognathus* or *Diademodon*.

A well-preserved femur (BMNH TR.8) from the Middle Triassic Manda Formation of Tanzania is a particularly important specimen because it is associated with a nearly complete pelvis. The material, found with lumbar ribs of a *Cynognathus-Diademodon* pattern, is generically indeterminate but many represent either *Alcodon* or *Scalenodon* (A. W. Crompton, pers. comm.).

Seeley (1895b: 146–147) described a femur which he referred to *Tribolodon frerensis*. Broom (1905a: 100–101) described a femur of *Diademodon mastacus*. Neither of these incomplete femora could be located for reexamination but from the available descriptions it appears that they conform morphologically to the femora described below.

Crompton (1955b: 628, 652, fig. 4) briefly described and figured the femur of *Cricodon metabolus* (UMC Field Catalogue No. 74) and made reference to the femur of *Scalenodon angustifrons* (UMC Field Catalogue No. 120A), both from the Manda Formation of Tanzania. Neither of these femora show any major differences from the *Cynognathus-Diademodon* pattern. von Huene (1950) also described femora from the Manda but all were disassociated and hence generically indeterminate.

The femur originally described by Parrington (1934: 57) as belonging to *Galesaurus* (UMC R.2722) lacked associated diagnostic cranial material and therefore may belong either to *Galesaurus* or to *Thrinaxodon*; it shows no differences from femora of *Thrinaxodon*.

MORPHOLOGY. The cynodont femur bears a distinct shaft which is moderately expanded at each end. The bone is straight except proximally where the shaft turns dorsomedially.

The head of the femur in *Thrinaxodon* is unossified. The proximal end is a flat, strap-shaped margin which runs in a hemicircle from the base of the (unossified) head to the greater trochanter (*h*, Fig. 49A,C). The margin is slightly expanded at the greater trochanter and widely expanded at the base of the head. There is no evidence that indicates that the head and greater trochanter were morphologically different from the better-ossified head and greater trochanter of larger cynodonts and therefore apparent differences are probably only artifacts of ossification.

In *Cynognathus* and *Diademodon* the proximal terminus from head to greater trochanter bears a rough texture typical of a cartilaginous cap. The head (*h*, Fig. 48C) is bulbous and somewhat oval in outline; its surface is confluent posteriorly with the crest leading to the greater trochanter, thus imparting a hemicircular outline to the proximal end of the bone. The amount of variation in the angle of the head among cynodont genera as cited by Crompton (1955b: 628) is probably spurious. Crompton claimed that in *Galesaurus*, *Glochinodontoides* and *Cynognathus* the head is only slightly reflected from the main axis of the shaft; in *Cricodon* and *Belesodon* the angle is supposedly greater while in *Traversodon* the angle is reputed to be 80°. However, as noted above, the head in *Thrinaxodon* and other small genera is unossified and therefore its orientation relative to the shaft cannot be determined with certainty. As preserved, the proximal end is truncated more or less transversely. This feature gives the appearance of little or no angle to the head. The femoral head in *Cynognathus* is quite unlike that in smaller cynodonts because much of it is ossified. The type, BMNH R.2571, is rather damaged and hence superficially appears to have little angulation. The femora of *Cricodon* (Crompton, 1955b: fig. 4) and *Belesodon* (von Huene, 1935–42: Pl. 15) are typical of larger cynodonts. The supposed greater angulation of *Traversodon* is almost certainly the result of postmortem damage to the incompletely ossified head. Similar distortions are often found in the femora of *Cynognathus* and *Diademodon*. The angle of the cynodont femoral head will be discussed in more detail in the following section.

The greater trochanter (*gr tr*, Figs. 48A,B,D; 49A,B,D), reflected dorsally, is slightly thicker than the ridge connecting it with the femoral head. The trochanter

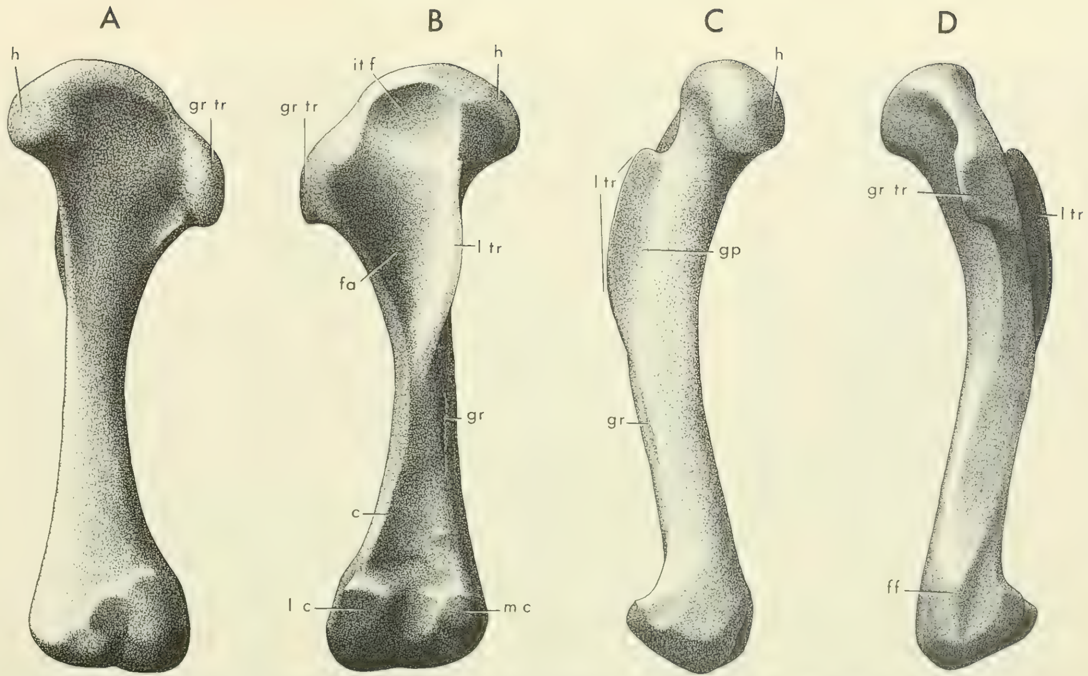
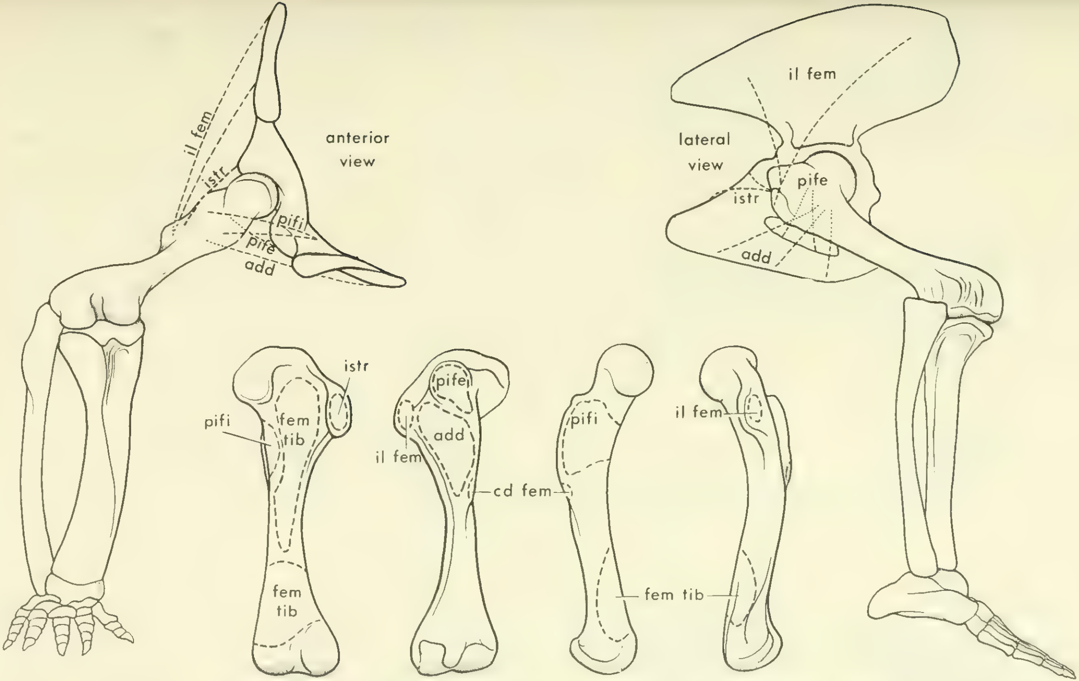


FIG. 48. Part I. Left femur of cf ?*Cynognathus* (?*Diademodon*) NMB C.2694 in A, dorsal; B, ventral; C, anteromedial; D, posterolateral views. X1. Abbreviations: *c*, crest between ventral and posterolateral surfaces of the femur; *fa*, fossa probably representing adductor musculature insertion; *ff*, point of femoro-fibular articulation; *gp*, groove between lesser trochanter and shaft, probably representing part of pubio-ischio-femoralis internus insertion; *gr*, groove of unknown function; *gr tr*, greater trochanter; *h*, femoral head; *it f*, intertrochanteric fossa; *l c*, lateral condyle; *l tr*, lesser trochanter; *m c*, medial condyle.


il fem
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tib
pife
il fem
add
cd fem
pifi
il fem
fem tib

FIG. 48. Part II. The line drawing depicts reconstructed muscle attachments and the presumed orientation of some of the thigh muscles. Additional abbreviations: *add*, adductor musculature; *cd fem*, caudo-femoralis; *fem tib*, femoro-tibialis; *il fem*, ilio-femoralis; *istr*, ischio-trocantericus; *pife*, pubo-ischio-femoralis externus; *pifi*, pubo-ischio-femoralis internus.

bears two surfaces: one facing dorsoposteriorly, probably for the insertion of the M. ischio-trochantericus, the mammalian homologue of the Mm. obturator internus and gemelli; the other facing posteroventrally for the insertion of the M. ilio-femoralis, homologous with the mammalian gluteals.

The proximal dorsal surface of the femur (Fig. 48A) is recessed below the margin of the head and greater trochanter and gave origin to part of the M. femoro-tibialis, homologue of the Mm. vasti of mammals. The area of origin is smooth and shallowly concave. Traced distally the concavity gradually attenuates and terminates at the posterodorsal aspect of the shaft's midpoint. A similar origin for the vasti may be discerned in *Thrinaxodon* (Fig. 49A) but due to the incomplete ossification of the greater trochanter the nature of the ilio-femoralis and ischio-trochantericus insertions cannot be determined.

All African cynodont femora have a round, deep intertrochanteric fossa on the ventral surface between the humeral head and the greater trochanter (*it f*, Figs. 48B, 49B). This fossa undoubtedly represents the insertion of the M. pubo-ischio-femoralis externus, believed by Romer (1922b: 571–572) to be homologous with the obturator externus and quadratus femoris. Later Romer (1924: 102) rescinded this opinion, expressing doubt that the intertrochanteric fossae of therapsids and mammals were homologous. The solution to the question ultimately depends on the question of homology of the lesser and internal trochanters (to be discussed in a later section). Romer (1922b: Pl. XLVI) incorrectly located the insertion of the pubo-ischio-femoralis externus in *Cynognathus* as lying between the greater and lesser trochanters; such a condition would be analogous to that in pelycosaurs but in cynodonts the fossa is relatively smaller and more proximally located. Romer's misinterpretation of the fossa position in *Cynognathus* was apparently due to the poor preservation of the type specimen. Romer was probably correct, however, in believing that the pubo-ischio-femoralis externus insertion extended onto the lesser trochanter. The fossa is clearly seen to extend up to the proximal end of the trochanteric crest but there is no evidence that the insertion extended distally along the crest.

The lesser trochanter is a prominent flange which arises abruptly near the head and runs distally along the anteroventral aspect of the shaft (*l tr*, Figs. 48C, 49C). The flange is highest at the middle where it is reflected slightly anteriorly (Fig. 48B). Descending gradually the trochanteric crest terminates at about the shaft midpoint. In galesaurids the crest is continued to the medial epicondyle as a sharp edge between the ventral and anterior surface of the shaft (Fig. 49B). A similar feature was noted by Haughton (1924: 89) in *Glochinodontoides* and by Broom (1932b: 279) in *Galesaurus*. In *Cynognathus* and *Diademodon* the anterior and ventral surfaces distal to the lesser trochanter are confluent, the boundary between them marked only by a short, narrow groove (*gr*, Fig. 48B,C). The relative height and length of the lesser trochanter is much greater than in pelycosaurs or in mammals and this raises questions as to the disposition of associated musculature. The anterior surface of the trochanter forms a shallow groove where it meets the femoral shaft (*gp*, Figs. 48C, 49C); this area probably afforded an insertion for the M. pubo-ischio-femoralis internus which, according to Romer (1922b: 565–566), is homologous with the mammalian iliacus, psoas and pectineus. The opposite (posterior) side of the trochanter is bounded by a broad fossa attenuating distally as the shaft narrows (*fa*, Figs. 48B, 49B). This fossa,

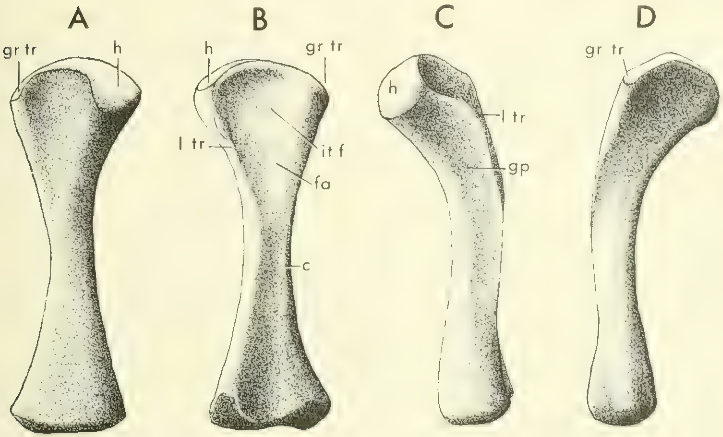


FIG. 49. Right femur of *Thrinaxodon*, SAM K. 1395, in A, dorsal; B, ventral; C, anteromedial; D, posterolateral views. X2. Abbreviations as in FIG. 48.

together with the posterior face of the trochanter, probably represents the insertion for the adductors which in living reptiles lies between the long flexors ventrally and the pubo-ischio-femoralis dorsally (Romer, 1922b: 571). The adductors probably did not extend distally beyond the midpoint of the shaft where the fossa terminates; in living reptiles the adductors are usually confined to the proximal half of the shaft whereas in mammals the insertion commonly extends distally almost to the origin of the gastrocnemius. Romer (1922b: Pl. XLVI) believed that the adductors in *Cynognathus* inserted in the shaft on the anterior side of the lesser trochanter. There are several reasons why such a reconstruction is less plausible than the one proposed above. First, Romer's figure of the ventral surface inaccurately portrays a ventrally facing surface anterior to the lesser trochanter onto which the adductors supposedly inserted. In fact the surface anterior to this trochanter faces anteriorly and provides no ventral surface for insertion. This area is occupied primarily by the M. pubo-ischio-femoralis internus as suggested above. Second, the adductor series inserts on the ventral aspect of the femur in recent lizards and mammals and the only analogous position in cynodonts is that suggested above. Moreover in *Dimetrodon* Romer and Price (1940: 149) recognized as well-developed adductor crest on the ventral surface of the femur between the fourth trochanter and the popliteal area. This contrasts to Romer's earlier, and I believe incorrect, interpretation (1922b: Pl. XLVI) in which the adductor insertion was reconstructed on the anteroventral aspect of the shaft adjacent to the fourth trochanter. From the adductor insertion in *Dimetrodon* as reconstructed by Romer and Price the adductor insertion of cynodonts and mammals can be derived without difficulty.

Romer (1922b: Pl. XLVI) showed that a fourth trochanter for the insertion of caudo-femoralis musculature is recognizable among most groups of Paleozoic tetrapods and also is retained in the Dinocephalia (e.g., *Moschops*) as a tubercle at the distal end of the lesser trochanter. The lesser trochanter of cynodonts occupies a relatively much greater length of the femoral shaft than it does in any pelycosaur or other Paleozoic tetrapod. The proportionate length in cynodonts is approximately equal to the combined lengths of the internal and fourth trochanters of those earlier tetrapods which possess both. Therefore it seems probable that cynodonts possessed caudo-femoral musculature inserting along the distal half of the crest. In one specimen in the BPI 1675 collection the distal extremity of the lesser trochanter bears an irregular conformation which might indicate an insertion of a separate muscle. Romer (1922b: 584 and Pl. XLVI) claimed that a coccygeo-femoralis insertion is not recognizable as such in *Cynognathus* and that in mammals the muscle is displaced onto the greater trochanter as the piriformis (see also Gregory and Camp, 1918: 497). There is no evidence of such a displacement in any known therapsid and it appears that the lesser trochanter of African cynodonts may represent a conjoined lesser and fourth trochanter. This view is further confirmed by the "trochanter minor" of *Exaeretodon* which displays two distinct tuberosities (Bonaparte, 1963a: 29). The proximal and lower of the two represents the lesser trochanter; the distal and higher tuberosity, homologous with the fourth trochanter, is located near the shaft midpoint but is connected with the lesser trochanter by a distinct crest. The very elongate lesser trochanter of *Chiniquodon* extends considerably distal to the middle of the shaft (Romer, 1969a: fig. 9); Romer interpreted this feature as an adductor ridge—a reasonable possibility.

In *Cynognathus* and *Diademodon* the posterior and ventral surfaces of the femoral shaft are separated along an angular intersection or crest which runs from the greater trochanter to the side of the lateral condyle (*c*, Fig. 48B). In galesaurids the same feature extends from the greater trochanter only to the middle of the shaft (*c*, Fig. 49B); distally the junction of ventral and posterior surfaces is more rounded and less angular. Broom (1932b: 279) described this feature in *Galesaurus*.

The femoral shaft of cynodonts is approximately square in cross-section through its center but distally it expands anteroposteriorly so that it is rectangular in cross-section. The expanded dorsal surface of the distal end as well as the adjoining anterior (medial) and posterior (lateral) aspects of the shaft probably gave origin to additional parts of the M. femoro-tibialis. The other part of this muscle, discussed above, took origin from the proximodorsal aspect of the femur. Romer (1922b: 564) showed that the femoro-tibialis was differentiated early in reptilian evolution and that its disposition in living reptiles and mammals (Mm. vasti) remains unchanged.

The distal end of the femur in larger cynodonts bears a robust lateral (posterior) condyle (*l c*, Fig. 48B) and a somewhat narrower medial (anterior) condyle (*m c*). The medial condyle projects further ventrally than does the lateral condyle. Both condyles articulate with the proximal end of the tibia and do not represent, as Crompton (1955b: fig. 4) indicated, separate tibial and fibular condyles. The distal terminal surface in galesaurids appears to have been extensively cartilaginous and is often preserved only as a broad convexity (Fig. 49B) which truncates the shaft perpendicularly. However, well ossified larger femora show that a large part of the distal articular surface for the tibia lies at 45° to the shaft axis (Fig. 48C; contrast to pelycosaurs in which the distal articular surface is more or less parallel to the shaft axis).

The fibular head probably articulated with the lateral epicondyle as in pelycosaurs but this joint cannot have transmitted much weight. In some femora a slightly rugose, raised area on the lateral epicondyle (*ff*, Fig. 48D) marks the site of the femoro-fibular articulation.

The femur of the South American traversodontid *Exaeretodon* (Bonaparte, 1963a) conforms with Karroo cynodont morphology except for the addition of a distinct ridge ventral and distal to the greater trochanter.

FEMORAL POSITION IN CYNODONTS

Gregory (1912), Gregory and Camp (1918), Romer (1922b) and Vialleton (1924) are to be credited for the concept of functional reorientation of the limbs during the reptile-mammal transition. Their work on the hindlimb presented broad morphological comparisons between diverse femora and attempted to reconstruct muscle attachments in selected fossil genera by determining muscle homologies in living reptiles and mammals. The general conclusion is that therapsid femora are functionally transitional between typical femora of the two classes and that "the changed position of the proximal segments is the key to the therapsid and mammalian type of locomotor apparatus" (Romer, 1922b: 600). These major conclusions have been incorporated into much of the paleontological literature but in fact were rather ambiguously stated and poorly documented. These authors openly admitted to the paucity and poor preservation of the cynodont material available. While the general thesis of a functional reorientation of the limbs is certainly valid, the mechanics of the transition are by no means clear. If such a transition took place among therapsids the cynodont femur, of which Gregory, Camp and Romer had only a proximal end, must be posturally as well as structurally intermediate between pelycosaurs and mammals. Accordingly in the following discussion the femoral orientation of pelycosaurs as well as cynodonts will be reviewed.

Ideally, reconstruction of limb posture requires an associated skeleton in which the articular facets are clearly preserved. Among cynodonts, complete or nearly complete skeletons are known only from the smaller forms (i.e., galesaurids) in which the cartilaginous ends of long bones are not preserved. Since articular surfaces are the most critical factor, disassociated but better ossified long bones of larger cynodonts offer the only possibility of postural reconstruction. The fact that the proportional ratios of hindlimb elements is not always exactly known does not detract from the basic conclusions drawn from the facet orientations. In the following discussion the stated orientation of articular facets is based on well preserved femora and tibiae in the Bernard Price (BPI 1675) and National Museum (NMB C.2694, NMB C.2696) collections. Femoral orientation with respect to the pelvis and acetabulum is interpreted from a generically indeterminate Middle Triassic cynodont (BMNH TR.8; ?*Alcodon* or ?*Scalenodon*).

The reconstruction of femoral posture rests on interpretation of three critical joints: acetabular, femoro-crural and cruro-pedal. In pelycosaurs the acetabulum is a shallow, laterally directed concavity (Fig. 50A); the femoral "head" is merely a broad

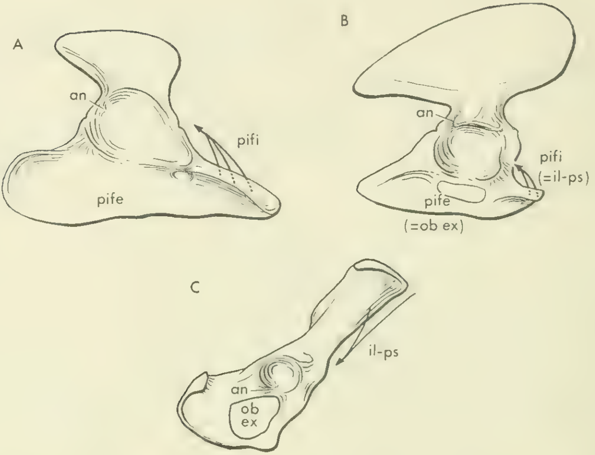


FIG. 50. Diagrammatic representation of the right half of pelves of A, a pelycosaur; B, *Cynognathus*; C, a mammal. *an*, acetabular notch; *il-ps*, ilio-psoas origin; *ob ex*, obturator externus origin; *pife*, pubo-ischio-femoralis externus origin, *pifi*, pubo-ischio-femoralis internus origin. Not to scale.

convexity on the distal end of the shaft (Fig. $54A_1$-A_3) but probably had a more rounded cartilaginous cap during life. There is no indication that the cartilaginous head was inflected medially or in any other direction. The articular surface as preserved truncates the shaft transversely to the shaft axis and probably indicates that the head was a bulbous, cartilaginous cap, the center of which lay on or near to the longitudinal axis of the femur. Therefore the femur must have projected laterally and nearly horizontally from the pelvis. Yet femoral position cannot be accurately determined from this articulation alone. The cruro-pedal articulation of pelycosaurs requires that the crus be directed ventrolaterally (Fig. 51A). The femoro-crural articulation is composed of the proximal tibial facets that are perpendicular to the long axis of the tibia and the femoral facets that are nearly parallel to the long axis of the femur, being directed primarily ventrally but also slightly laterally. This articulation also requires that the crus be directed ventrolaterally, but it requires a less oblique orientation (relative to the sagittal plane) than does cruro-pedal articulation. If the femur were held horizontally, the crus would be almost vertical, but then the distal end of the crus could not articulate with the pes. The solution to the apparent disparity in facet orientations requires that the distal end of the femur be slightly elevated above the proximal end (Figs. 51A; *dashed line*, 52B), a conclusion evidently reached by Romer (1922b: fig. 7).

Compared with the pelycosaurian pattern the hip, knee and ankle joints in cynodonts are substantially altered. At the knee joint the tibial facets transversely truncate the proximal end of the tibia, as in pelycosaurs. However, the distal femoral facets for the tibia are no longer parallel to the femoral axis as in pelycosaurs but are inclined to an angle of about 45° to the femoral axis (see above, p. 172). This signifies that the distal end of the femur was held in a position lower than the level of the acetabulum (Figs. 51B, *heavy line*; 52B). Yet the cynodont condition is not more mammalian than

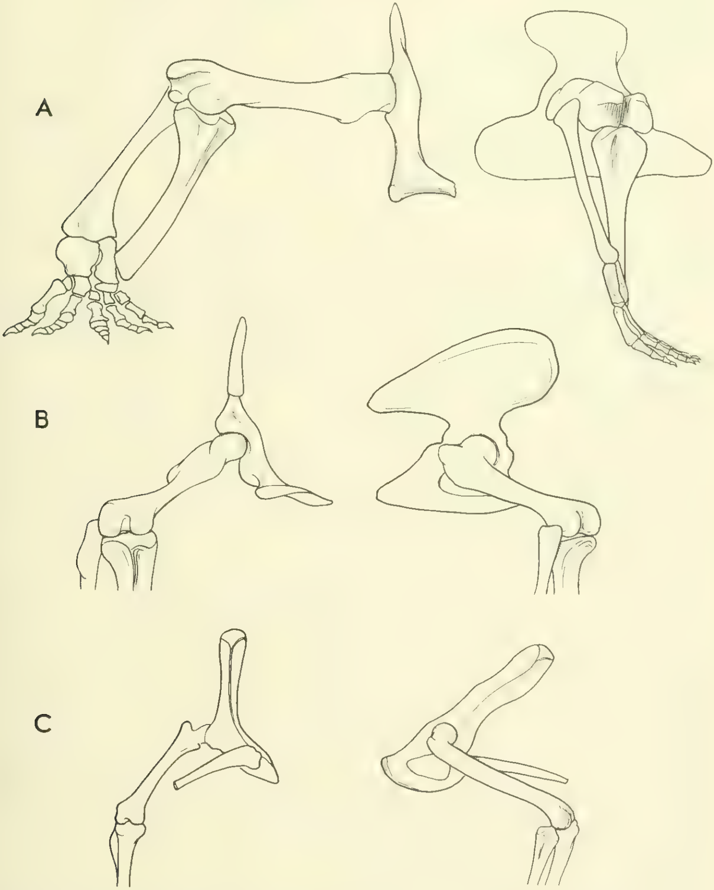


FIG. 51. Pelvis and hindlimb orientation as reconstructed in A, a pelycosaur and B, a cynodont compared with that in C, a mammal. On the left are anterior views, on the right lateral views. Not to scale.

the pelycosaur condition by virtue of the more distal (rather than ventral) orientation of the femoral facets. In most non-specialized mammals the distal articular facets represent a 90° arc from the ventral to the distal aspects of the femur. This wide arc permits a large amount of flexion and extension and is often further increased in cursorial specialization. In cynodonts the distal articular facets are intermediate—neither entirely distal nor ventral—but the orientation is a stage in the development of a mammalian type of facet for increased flexion and extension. The presence of cartilage on these facets in cynodonts could possibly have formed an arc essentially like that of mammals.

The major alteration in the cruro-pedal (ankle) joint of therapsids and of cynodonts in particular will be discussed in a following section. But to summarize, the evolution of a plantigrade pes was accompanied by a more vertical cruro-pedal relationship; this contrasts to the pelycosaurian condition in which the crus extended ventrolaterally to reach the tarsus (cf. Fig. 51A and B).

Neither the femoro-crural nor cruro-pedal articulations in cynodonts define precisely the posture of the femur, however. The morphology of the acetabulum and femoral heads are the determining factors in this regard. The pelvis of BMNH TR.8, although somewhat flattened (post-mortem) mediolaterally, demonstrates that the cynodont acetabulum had advanced toward the circular, deep socket form of mammals (Figs. 46A, 50). In life the iliac facet of the cynodont acetabulum probably projected farther laterally than either the pubic or ischial facets. This interpretation is based upon undistorted ilia (NMB C.2699) in which the pubic and ischial processes of the ilium are inflected medially. Consequently the rims of the pubic and ischial facets lay medial to the iliac facet (see Fig. 45B) and the acetabulum may be regarded as facing somewhat ventrally as well as laterally. Of course in mammals the acetabulum is also directed slightly ventrally concomitant to the more vertical orientation of the femur. The pelvis of BMNH TR.8 also shows that the pubic facet does not project as far laterally as the ischial facet. This feature is probably related to the anteriorly directed position of the cynodont femur.

The cynodont femoral head is not round and hemispherical as in mammals but is rather oval and bulbous (Figs. 48, 54B_3). Furthermore the center of the head is not located on line with the axis of the shaft as it is in pelycosaurs but projects medially and dorsally. A quantitative estimate of the position of the femoral head of cynodonts relative to that in pelycosaurs and mammals now can be made with some degree of confidence. The orientation of a femoral head may be represented as a plane tangential to a point on its surface which is equidistant from the periphery. The orientation of the femoral head may then be expressed as an angle relative to the longitudinal axis of the femur. In cynodonts with well-ossified femoral extremities this angle appears to have been on the order of 55° compared with the 80° orientation in pelycosaurs or a typical mammalian angle of 25° (Fig. 52A). The "head" of the pelycosaurian femur is never more than a broad convexity on the proximal end; for reasons noted above the femur projected laterally and the head was undoubtedly a cartilaginous cap set perpendicularly to the shaft. The intermediate position of the cynodont femoral head is indicative of a shift toward a more mammalian femoral posture. Specifically, the angle between the long axis of femur and the parasagittal plane (*vertical line*, Fig. 52A) becomes more acute. In generalized, non-cursorial mammals the femur usually

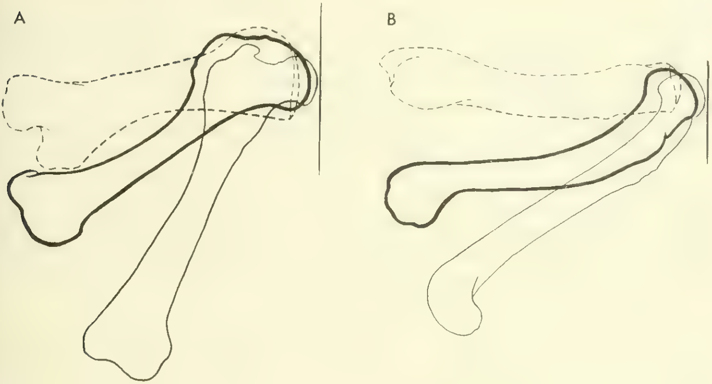


FIG. 52. A, dorsal views: B, anterior views of femoral posture in pelycosaurs (dotted line), cynodonts (heavy line), and generalized mammals (narrow line). The vertical line in both A and B represents a parasagittal plane through the deepest part of the acetabulum. Not to scale.

projects obliquely away from the body axis at angles of 20 to 25°. Thus the cynodont femur occupies a truly intermediate position between that of primitive synapsids and their mammalian descendants.

The cynodont femur, viewed from either medial or lateral aspect, shows that the proximal end and head are reflected dorsally relative to the rest of the shaft (Fig. 52B). This condition, apparently absent or little developed in pelycosaurs, is retained by generalized mammals although not in such extreme form (Fig. 52B). Thus the cynodont and mammalian femoral head is directed not only medially but also dorsally. The functional significance of this feature appears to be related to the evolution of a mammalian pattern of femoral posture and movement.

In pelycosaurs forward thrust was transmitted to the pelvis as the femur swung posteriorly in a horizontal arc. But even in its most posterior position the femoral axis probably did not form an angle smaller than 45° with the body axis because neither the head of the femur nor the acetabulum appear to have been sufficiently rounded to permit such a posture. At no point in the locomotory cycle was the femoral head directed more anteriorly than medially; thus transmission of forward thrust was mechanically inefficient and undoubtedly relied on strong ligamentous and perhaps muscular control of the forces generated. At any time during the propulsive stroke, medially directed components comprised a significant part of the total force generated.

Among therapsids the inefficiency of the pelycosaurian type of femoral head would have been rendered more acute by the tendency to shift the femur beneath the body, i.e., by displacing its distal end anteriorly and ventrally. In such a position a head situated on the proximal end and perpendicular to the shaft axis is poorly suited to transmit forward thrust. Therefore the cynodont femoral head develops medially to compensate for the anterior displacement of the distal end of the shaft. The dorsal reflection of the head, however, is a function of the ventral displacement of the distal end of the shaft. As the distal end of the femur swings ventrally and posteriorly during locomotion a forward and upward thrust is transmitted to the acetabulum. However, the cynodont femur is not aligned with the body axis at an angle of 25° or less, as in mammals, but instead lies at about 55°. This intermediate posture results in an arc of femoral movement which is neither nearly horizontal, as in pelycosaurs, nor nearly vertical, as in mammals. As a result the femur must bear propulsive forces on the dorsal aspect of its proximal end necessitating a somewhat dorsally directed femoral head.

In some generalized, non-cursorial mammals a slight dorsal reflection of the femoral head is retained. It is apparently correlated with a femoral posture in which there is a relatively large angle (approximately 25° or more) between the femoral and body axes. In other mammals whose femora are posturally less oblique to the body axis the dorsal reflection of the head is altogether lost.

THE HOMOLOGY AND FUNCTIONAL EVOLUTION OF THE MAMMALIAN LESSER TROCHANTER

Questions of homology between various trochanteric structures of the femur have always been of paleontological interest because trochanters mark the insertion of major pelvic muscles. Homologous trochanters imply homologous musculature although not necessarily similar functional patterns. The homology of trochanters in fossil forms is therefore a basic consideration in interpreting functional anatomy; if trochanters occur in an analogous position on femora of related species but are not considered to be homologous, the question is immediately raised as to why one replaced the other.

The homology of the internal trochanter (trochanter internus) of reptiles and the lesser trochanter (trochanter minor) of mammals has been both accepted and rejected primarily on the basis of fossil evidence. The lesser trochanter of mammals is principally the site of insertion of ilio-psoas musculature which is particularly important in protracting (or flexing) the femur. The lesser trochanter in typical position lies below the level of the acetabulum, and since it occurs on the medial aspect of the shaft, it is positioned nearly beneath the acetabulum as well. The internal trochanter of living reptiles is associated principally with the insertion of a major adductor muscle, the pubo-ischio-femoralis externus. With regard to its position relative to other femoral features, the internal trochanter is analogous to the lesser trochanter. It lies below the level of the acetabulum but because reptilian femora are oriented more horizontally than vertically the trochanter lies lateral to the acetabulum rather than directly beneath it. Nevertheless the internal trochanter lies on the anteroventral aspect of the reptilian femur which is the morphological equivalent of the medial aspect of the mammalian femur. In the following review of the evolution and homology of the mammalian lesser trochanter, the term "anteroventral trochanter" is applied to those trochanters of fossil forms which are in the position of an internal (reptilian) or a lesser (mammalian) trochanter but which cannot be positively designated as either.

Gregory (in Gregory and Camp, 1918: 534) accepted the homology between the reptilian internal and the mammalian lesser trochanter. He cited the fact that the trochanter in reptiles is associated with the insertion of the pubo-ischio-femoralis internus and externus muscles, whereas in mammals the apparent homologue of the pubo-ischio-femoralis internus, the ilio-psoas, inserts on the lesser trochanter. The fact that the obturator externus, the mammalian homologue of the pubo-ischio-femoralis externus, did not insert on the trochanter (as in reptiles) was not discussed.

Romer (1922b: 566) concluded that the internal trochanter is only the "partial homologue" of the lesser trochanter because, as first shown by Gregory, the muscular insertions of homologous muscles were not exactly similar in relation to the trochanter. Later Romer (1924) entirely rejected the homology between the reptilian internal and the mammalian lesser trochanter. Romer's conclusion, based largely on fossil evidence, has never been challenged. Howell's (1941) detailed comparative study confirmed Romer's conclusions that the reptilian internal trochanter and the mammalian lesser trochanter are not homologous because they represent the attachments of non-homologous muscles. Howell emphasized that the internal trochanter of living reptiles such as *Iguana* is associated with muscles of tibial and obturator innervation, whereas the lesser trochanter of mammals represents the attachment of muscles of femoral innervation. Howell was careful to point out, however, that living reptiles are specialized myologically, and "have probably departed farther from basic reptiles in the plan of their hip musculature than have mammals". The point of interest therefore is no longer the question of homology between internal and lesser trochanters but the evolutionary development of the latter. Parrington (1961) adduced evidence to support the view that cynodonts had a mammalian lesser trochanter and that the supposed transition from a pelycosaurian internal trochanter occured during a pre-cynodont stage. Romer and Price (1940) had previously concluded that the pelycosaurian internal trochanter represents the attachment of the pubo-ischio-femoralis externus muscle, and thus is homologous with the internal trochanter of living reptiles. If both Romer and Price (1940) and Parrington (1961) are correct, then a major change in trochanter morphology occured between pelycosaurs and cynodonts with the lesser trochanter replacing the internal trochanter. Such a change might be expected to accompany the development of an essentially mammalian type of pelvis. However, the paleontological evidence, discussed below, does not support the view that the supposed origin of the mammalian lesser trochanter was accompanied by the evolution of a typically mammalian system of pelvic musculature. In order to present a comprehensive survey of this evidence, a summary and critique of both Romer's and Parrington's contributions must be given.

Romer (1924) established that the trochanteric structure of a primitive therapsid such as *Deuterosaurus* is basically similar to that of pelycosaurs. Basing a reconstruction of musculature on the condition in living reptiles, *Iguana* in particular, Romer concluded that in pelycosaurs and primitive therapsids the pubo-ischio-femoralis externus inserts into the intertrochanteric fossa and on the adjacent internal trochanter (*pife*, Fig. $54A_2$). The association of the trochanter and fossa with the same muscle insertion is particularly clear in some pelycosaur femora where a rugosity may be traced from the fossa to the trochanter. The muscle interpreted to have inserted here took origin from the lateral aspect of the pubo-ischiadic plate (*pife*, Fig. 50A). Romer further concluded that the pubo-ischio-femoralis internus in both therapsids and pelycosaurs inserted on the dorsoproximal and anteroproximal surface of the shaft; in pelycosaurs, at least, this area extends from near the ilio-femoralis insertion (the site of the greater trochanter in mammals) anteriorly and then ventrally across the anterior face of the internal trochanter (*pifi*, Fig. $54A_1$). In cynodonts, however, the exact disposition of the insertion is rather conjectural. Romer claimed that a femur of *Diademodon* has a muscle scar on the anterodorsal aspect of the proximal end which delimits the border between the pubo-ischio-femoralis internus (or ilio-psoas) and the iliofemoralis (gluteal) muscles, the latter inserting on the greater trochanter. According to this interpretation the pubo-ischio-femoralis internus inserted anterior to the greater trochanter, but Romer did not state whether he believed the insertion extended anteroventrally onto the face of the internal trochanter. Romer's ultimate contention was that this muscle scar represents the incipient lesser trochanter which subsequently migrated anteroventrally to take the place of the internal trochanter.

Parrington (1961: 295) reported that the supposed pubo-ischio-femoralis internus insertion of Romer could not be identified on any of the well-preserved cynodont femora available. Similarly, this feature was not present on any of the many cynodont femora examined during the course of this study. Nevertheless the absence of this feature does not obviate the possibility that the pubo-ischio-femoralis internus insertion in cynodonts was similar to that in pelycosaurs—which in essence is Romer's conclusion (*pifi*, Fig. $54B_1$).

The crux of Romer's argument is based on the apparent difficulty in explaining "the diverse tendencies [of trochanter location] seen in a morphological series of femora" (Fig. 53). Romer attempted to show that the internal trochanter of therapsids displaces posteriorly and diminishes in size during the pelycosaur-therapsid transition (Fig. 53A–C). Then the trochanter enlarges and displaces anteriorly (Fig. 53D) at the monotreme level of organization. Finally, the trochanter moves ventrally and anteriorly again among therian mammals (Fig. 53E,F). Since it is difficult to account for two reversals in the evolutionary continuum from pelycosaurs to mammals, Romer concluded that the internal trochanter moved posteriorly and finally was lost, only to be

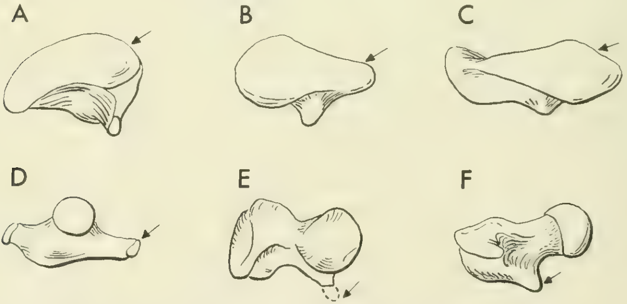
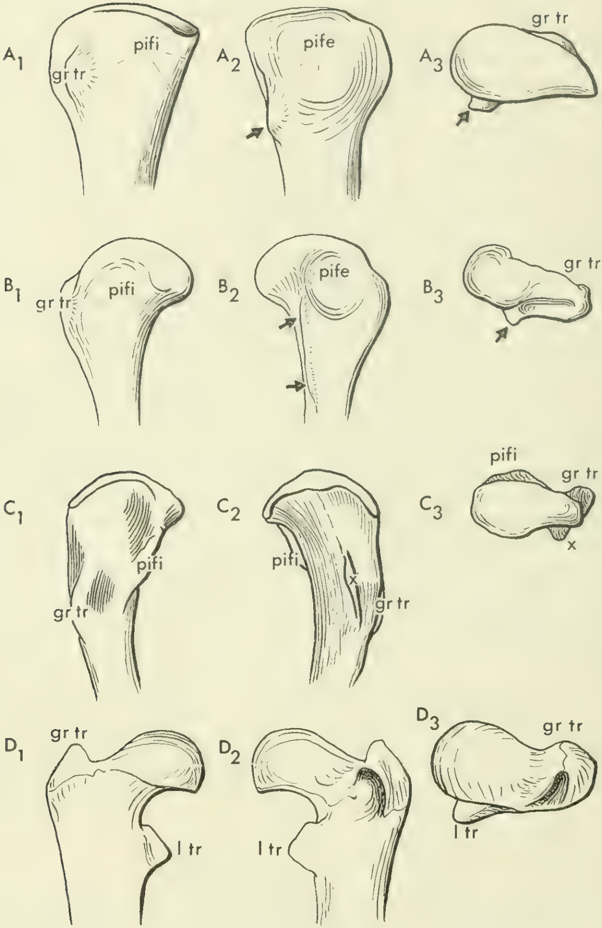


FIG. 53. The evolution of the trochanter minor of mammals as interpreted by Romer (1924). The arrow indicates the insertion of the ilio-psoas and homologues and, according to Romer, represents the mammalian trochanter minor or its homologue. After Romer, 1924: fig. 3. A, *Dimetrodon*; B, *Deuterosaurus*; C, *Cynognathus*; D, *Ornithorhynchus*; E, *Pachyaena*; F, modern placental. Not to scale.

replaced by a lesser trochanter which migrated ventrally from the dorsoproximal surface. Therefore the trochanters in question are not homologous between synapsids and mammals.

Romer's evidence for a de novo origin of the mammalian lesser trochanter is inconclusive because it fails to demonstrate that a vestigial internal trochanter and an incipient lesser trochanter coexisted in some transitional therapsid. Parrington (1961) attempted to provide just such a piece of evidence by a comparative study of therapsid femora. Parrington recognized that theriodont femora may be grouped into three taxonomic-morphologic categories: 1) titanosuchids and gorgonopsids; 2) therocephalians and primitive bauriamorphs; and 3) cynodonts and tritylodonts. The femora of the cynodont *Cricodon* and the tritylodonts *Bienotherium* and *Oligokyphus* make a convincing morphological series between the cynodont and the monotreme condition. On this account Parrington concluded that the cynodont trochanter is homologous with the mammalian lesser trochanter and that the internal trochanter to lesser trochanter transition occurred among more primitive therapsids. Since cynodonts are the only advanced therapsid group known from which, on evidence of cranial osteology and dentition, mammals could have been derived, Parrington's deduction is logical. However, if the cynodont trochanter on the anteroventral aspect of the shaft is the lesser trochanter then the expected arrangement of the pubo-ischio-femoralis internus muscle should be that of its mammalian homologue, the ilio-psoas group. To the contrary, the pelvic conformation of cynodonts suggests that a basically pelycosaurian pattern was retained. In pelycosaurs the pubo-ischio-femoralis internus probably arose from the medial aspect of the pubic plate just as in living reptiles where there is often a distinct shelf (Romer, 1922b: 565–566; *pifi*, Fig. 50A). An analogous shelf is present in cynodonts (Fig. 50B). In mammals the ilio-psoas group takes origin from the lumbar vertebrae and either an external, anteroventrally facing shelf on the ilium (*il-ps*, Fig. 50C) or the internal surface of the ilium. There is no indication of such a shelf on the flat, plate-like cynodont ilium, despite the claim by Parrington, who recognized this difficulty, that the height of the iliac blade "invites the interpretation that ventrally it accommodated the iliacus, or combined iliaco-psoas muscle, in the mammalian manner" (Parrington, 1961: 288). The internal surface of the ilium could not have been the site of origin for a mammalian iliacus because it was occupied by the extensive sacroiliac articulation. Contrary to Parrington, the shape of the cynodont ilium is here construed as evidence that the ilio-psoas muscles were not disposed in a mammalian fashion. This interpretation leads to an apparent paradox: cynodonts possessed a mammalian lesser trochanter but retained a basically reptilian origin for the muscles that are associated with this trochanter in mammals.

Parrington correctly regarded the anteroventral trochanter of titanosuchian and gorgonopsid femora as being homologous with the similarly located trochanter of pelycosaurs. The transition from an internal trochanter to a lesser trochanter according to Parrington's view is represented by the femora of a Late Permian whaitsid therocephalian and an Early Triassic scaloposaurid bauriamorph. Parrington's whaitsid femur (Fig. 54C) shows a posterodorsal proximal trochanter identified as the greater trochanter (*gr tr*, Fig. 54C) and a posteroventral trochanter immediately beneath it identified as the internal trochanter (*x*, Fig. $54C_2$,C_3). Near the proximal end of the shaft along its anterodorsal aspect is a ridge that Parrington regarded as marking the point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gr tr
l tr

FIG. 54. Proximal ends of the femora of A, *Dimetrodon*; B, *Cynognathus*; C, a whaitsid therocephalian; D, *Didelphis*. C after Parrington, 1961: fig. 7 and a cast of this specimen. Subscript 1, dorsal views; subscript 2, ventral views; subscript 3, proximal views. Arrows indicate the anteroventral trochanter, variously considered the (reptilian) trochanter internus or (mammalian) lesser trochanter. Abbreviations: *gr tr*, greater trochanter; *l tr*, lesser trochanter; *pifi*, pubo-ischio-femoralis internus insertion; *pife*, pubo-ischio-femoralis externus insertion; *x*, the supposed trochanter internus as identified by Parrington. Not to scale.

of pubo-ischio-femoralis internus insertion (*pifi*, Fig. 54C). The femur of a scaloposaurid bauriamorph bears the same features as the whaitsid femur. Both forms would appear to substantiate Romer's (1924) claim that the internal trochanter migrated posteriorly in therapsids and its original position was occupied by a lesser trochanter that migrated ventrally from the anterodorsal aspect of the shaft.

However, there are several objections which may be raised against Parrington's interpretation. First, there is no evidence that the figured femora represent forms ancestral to cynodonts. The bauriamorph from the Early Triassic is certainly too late and the whaitsid from the Late Permian is at least contemporaneous with the earliest cynodonts. The phylogenetic relationship of the therocephalians and bauriamorphs to the cynodonts is by no means established. Parrington recognized this fact in his diagrammatic representation of therapsid evolution; the therocephalians are tentatively considered to have been derived from titanosuchids and bauriamorphs from the therocephalians, but the question of cynodont ancestry is left open.

A second question raised by Parrington's hypothesis is whether the figured femora represent a morphologically intermediate type between primitive and advanced therapsids or whether the femora are morphologically specialized. In view of the doubtful relationship of the whaitsids and scaloposaurids to cynodonts there is no substantial proof that the femoral trochanter morphology is intermediate. The case can be argued that whaitsid and scapolosaurid femora are peculiarly specialized and the critical question here concerns the identification of the internal trochanter. According to Parrington the internal trochanter lies beneath and is more or less a direct continuation of the greater trochanter. However, Parrington's internal trochanter might simply represent a ventral enlargement of the greater trochanter. In this case the true internal trochanter is lost. This interpretation is made more plausible by the fact that a parallel development occurred in anomodonts; the internal trochanter of dinocephalians is reduced and is altogether absent in dicynodonts (Parrington, 1961: 291). But anomodonts did not develop a true lesser trochanter (i.e., a pubo-ischio-femoralis internus trochanter) that shifted from a primitive dorsal to a ventral position. Therefore the loss of the internal trochanter need not be directly related to the origin of a lesser trochanter. I find no convincing evidence to support the interpretation that the pubo-ischio-femoralis insertion on whaitsid and scaloposaurid femora was located in any other but the primitive anterodorsal position.

Even if Parrington's identification of the whaitsid and scaloposaurid trochanter internus is correct (i.e., *x* in Fig. 50C representing the pubo-ischio-femoralis externus insertion), the pubo-ischio-femoralis internus insertion in both forms retains only the dorsal part of its primitive position and shows no tendency toward ventral displacement. In fact the apparent restriction of the insertion to the dorsal surface might be interpreted as a specialization. In pelycosaurs the insertion is marked by an area of rugosity which covers both the dorsal and anterior (medial) aspects of the shaft (Fig. 54A_1; see MCZ 1969, a *Dimetrodon* femur). According to Parrington's interpretation only the dorsal area of insertion is present in whaitsids and scaloposaurid femora.

There is no disputing the fact that the internal trochanter of reptiles is not the homologue of the mammalian lesser trochanter; it is clearly established that different muscles attach to each. The point of dispute is how the mammalian pattern arose. Romer's (1924) hypothesis of trochanter migration is based on an incorrect assessment of the trochanter position in cynodonts and on the dubious view that the lesser trochanter position in monotremes is truly primitive. Parrington's attempt to further document Romer's hypothesis fails to demonstrate the probability of migration of the pubo-ischo-femoralis internus insertion. An alternate possibility remains, that an anteroventral trochanter has always been present on the femora of synapsids which were on or near to the line of mammalian ancestry and that the muscular relations of the anteroventral trochanter changed during the evolution of the mammalian locomotory system. In pelycosaurs the insertions of the pubo-ischio-femoralis internus extended to the anterior (medial) face of the anteroventral trochanter (Fig. $54A_1$) but not to its apex. The apex of the anteroventral trochanter was probably occupied by the pubo-ischio-femoralis externus as was the adjacent intertrochanteric fossa (Fig. $54A_2$). In mammals the obturator externus (the pubo-ischio-femoralis externus homologue) does not insert onto the anteroventral trochanter but is confined to the intertrochanteric fossa. The iliacus and psoas muscles (the pubo-ischio femoralis internus homologue) apparently have gained an insertion on the apex of the trochanter. The hypothesized shift in attachments is slight because the ilio-psoas homologue in pelycosaurs (pubo-ischio-femoralis internus) is interpreted to have inserted partly on the anterior aspect of the anteroventral trochanter (Fig. $54A_1$). This hypothesis requires no trochanter migration, disappearance or de novo origin for which there is no evidence in mammalian ancestry.

The hypothesized shift in the muscular relationships of the anteroventral trochanter appears to be related to basic changes in femoral orientation and excursion between early synapsids and mammals. The obturator externus and ilio-psoas will be considered separately in this regard. The pubo-ischio-femoralis externus (or obturator externus) of pelycosaurs was probably a relatively large adductor acting across the ventral aspect of the hip joint. Adduction of the femur among early synapsids was most likely the principle mechanism for elevating the body off the ground during locomotion. In mammals the adductor function and orientation of the obturator externus appears to have been retained essentially unchanged. However, less adductor effort to maintain an elevated body position would be required by a mammalian posture with femora in a more or less parasagittal plane than by an early synapsid posture with femora in a more or less horizontal plane. For this reason it appears that the obturator externus, among other adductors, plays a less important postural role in mammals than in early synapsids. The relative diminution of the interochanteric fossa and the interpreted recession of the obturator externus from the anteroventral trochanter are here constructed as sequelae to the relative decrease in functional importance of the obturator externus for mammalian posture.

The pubo-ischio-femoralis internus of pelycosaurs is interpreted as having taken origin from the medial surface of the pubis and as having inserted onto the anterior aspect of the anteroventral trochanter and the dorsal aspect of the proximal shaft (*pifi*, Figs. 50A, $54A_1$). The origin and insertion lie at approximately the same horizontal level. Thus reconstructed, this muscle is likely to have functioned as a femoral protractor by swinging the femur forward in a more or less horizontal arc. The homologous musculature in mammals, the ilio-psoas group, also functions as a femoral protractor (or, in more common usage, flexor of the thigh) but with the important difference that femoral excursion is in a nearly parasagittal rather than a horizontal plane. The apparent dorsal migration of the ilio-psoas group from its primitive attachment to the pubis (as the pubo-ischio-femoralis internus) is explicable in terms of introducing an upward component to femoral flexion. The shift of ilio-psoas insertion onto the anteroventral trochanter appears to be related to the development of an inflected femoral head and the resultant repositioning of the mechanical axis. In mammals the mechanical axis passes through the femoral head and between the tibial condyles (Fig. 55A_1). If the ilio-psoas had remained in a position analogous to that in pelycosaurs—on the anterior and dorsal aspect of the proximal shaft (Fig. 55B)—the insertion would lie lateral to the mechanical axis. Such an arrangement would engender a substantial rotational component to ilio-psoas action and the result of both flexion and rotation might appear as in Figure 55B. However, the migration of ilio-psoas insertion onto the apex of the lesser trochanter eliminates any major rotational component because the insertion lies approximately on the mechanical axis. Flexion alone results. Although there has been longstanding controversy over the possible rotational actions of the ilio-psoas, electromyography in humans, at least, has demonstrated that no rotational components exist (Basmajian, 1967: 206–209). Insertion of the ilio-psoas onto the lesser trochanter thus appears to be an arrangement to produce flexion of the thigh without rotation—the simplest movement to advance the femur in a nearly parasagittal plane.

In conclusion, it seems likely that there has always been an anteroventral trochanter (an internal trochanter or a lesser trochanter) in synapsids that were on or close to the line of mammalian ancestry. In the more primitive forms the trochanter was associated primarily with the pubo-ischio-femoralis externus and to a lesser extent with the pubo-ischio-femoralis internus. In later forms the pubo-ischio-femoralis internus became inserted primarily on this trochanter in conjunction with the requirements of a more mammalian posture and femoral movement. It cannot be determined with certainty in which pre-mammalian form or forms the pubo-ischio-femoralis internus occupied it exclusively. It would seem that this shift would be accomplished by the development of the mammalian form of pelvis. The earliest pelvis of a mammalian pattern is

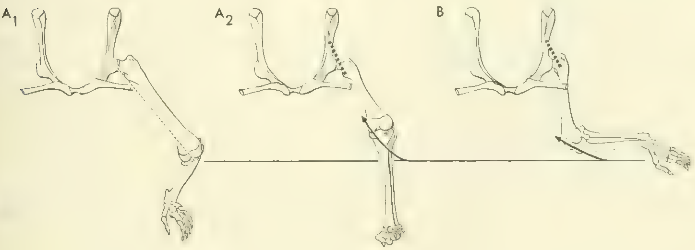

FIG. 55. Pelvis and hindlimb of a mammal in anterior view to demonstrate the action of ilio-psoas musculature. Insertion of this musculature on or near the lesser trochanter flexes the femur from a position in A_1 to a position in A_2. If the ilio-psoas musculature had retained its primitive insertion on the dorsum of the femur, flexion would be accompanied by counterclockwise rotation, resulting in the bizarre position illustrated in B. The horizontal line provides a plane of reference. Thick dashed line indicates position and insertion of ilio-psoas; thin dashed line indicates position of the mechanical axis of the femur.

known among the tritylodontids (e.g., *Oligokyphus*; Kühne, 1956) which are derivatives of advanced cynodonts but are not mammalian ancestors. In these forms the lesser trochanter has assumed a recognizably mammalian shape.

TIBIA (Figs. 56, 57)

MATERIAL. With the exception of size and minor proportional differences, cynodont tibiae are very much alike. The tibia in *Thrinaxodon* is known from specimens listed by Brink (1954) and from BPI 376 and BPI 287. The most complete of available specimens is SAM K.1395.

Tibiae of *Cynognathus* and *Diademodon* are preserved in two collections (BPI 1675; NMB C.2696). The two genera cannot be distinguished on the basis of tibial morphology. The supposed tibia of *Gomphognathus* (=*Diademodon*) *kannemeyeri* (SAM 977) may be either *Diademodon* or *Cynognathus*.

A crushed right tibia (DMSW R. 189), possibly but not certainly referable to *Diademodon*, was recovered in association with a right fibula. This is one of the few specimens in which it is possible to examine the crural elements of the same individual.

Parrington (1934) described fragmentary tibiae from a specimen (UMC R.2722) supposed to be *Galesaurus* but which, lacking associated cranial remains, could just as probably be *Thrinaxodon* (see above p. 62).

MORPHOLOGY. The shaft of the cynodont tibia is anteroposteriorly flat and bowed slightly medially (Figs. 56, 57). The proximal end expands laterally and somewhat anteriorly to support a large articular surface. The distal end expands in a similar fashion but less extensively. As a result of this expansion the lateral margin of the tibia is markedly concave while the medial margin is only slightly so. Likewise the anterior (extensor) surface is somewhat concave while the posterior (flexor) surface is straight.

The proximal articular surface, irregularly oval in outline, bears two oval facets for articulation with the femoral condyles (*pr ar f*, Fig. 56A,C). Both facets are slightly concave and are separated by a low ridge running posteromedially. The anteromedial facet, inclined anteromedially with its axis transverse, contacts the medial (smaller) femoral condyle. The laterally inclined lateral facet, with its axis running posteromedially, contacts the lateral (larger) femoral condyle. The posteromedial corner of the articular surface is convex and is continuous with the ridge separating the condyles. A tubercle projecting from the anteromedial margin of the articular surface (*tb q*, Fig. 56A) may represent the insertion of quadriceps musculature; a similar and apparently homologous tubercle occurs on pelycosaur tibiae (Romer and Price, 1940: 156). Medial to this tubercle is another smaller tubercle (*tb*, Fig. 56A) which is absent, or at least unossified, in galesaurids. Between the two tubercles the rim of the proximal facet is emarginated and pulley-like. Possibly a ligament or tendon crossed this point between the femur and the lower leg.

The tibial shaft is flattened anteroposteriorly and is thus clearly divided into extensor (anterior) and flexor (posterior) surfaces. The extensor surface as a whole is rather flat except for a ridge which transverses the shaft obliquely from medial to lat-

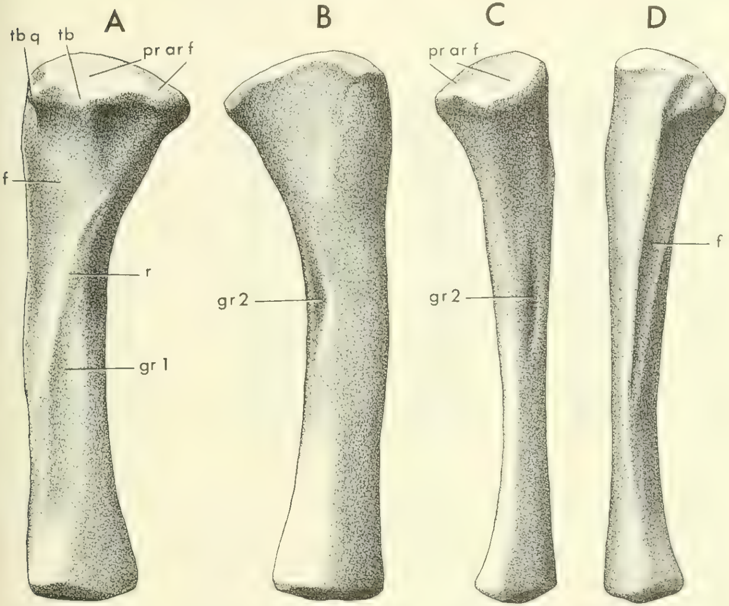

FIG. 56. Left tibia of cf. ?*Cynognathus* (?*Diademodon*), NMB C.2696, in A, anterior; B, posterior; C, lateral; D, medial views. X2/3. Abbreviations: *f*, fossa possibly representing the origin of a pedal dorsiflexor; *gr 1*, *gr 2*, grooves of uncertain function; *pr ar f*, proximal articular facets; *r*, ridge of uncertain function; *tb*, tubercle of uncertain function; *tb q*, tubercle possibly for quadriceps insertion.

eral aspect (*r*, Figs. 56A, 57A) Proximomedial to this ridge the extensor surface bears a shallow but distinct fossa of uncertain function (*f*, Figs. 56A,D, 57A) ; possibly it represents the origin of a pedal dorsiflexor. Both fossa and ridge disappear upon reaching the medial margin of the shaft which separates extensor and flexor surfaces. Undoubtedly both features are related to extensor muscle attachment, but it is uncertain which muscle or muscles are most likely to have been involved. The distal half of the extensor surface is flat except that in well-ossified specimens a slight groove can be detected (*gr 1*, Fig. 56A). This groove runs distally from the midpoint of the oblique ridge and extends to the distal end where it is terminated by the swelling of the distal articular facet rim. The only muscular association with this groove might possibly be a short digital extensor, but the usual origin for such a muscle in recent tetrapods is fibular and thus a proposed tibial origin for cynodonts is suspect.

Flexor and extensor surfaces adjoin medially along a sharply defined ridge (Figs. 56D, 57C). In well-ossified tibiae a tubercle occurs on the proximal end of this ridge. Flexor and extensor surfaces are separated laterally along their proximal half by a well-

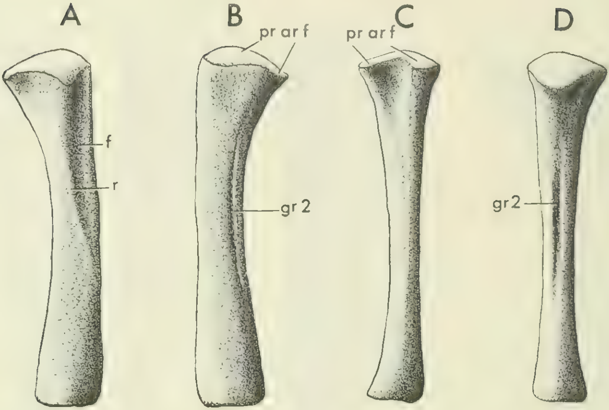

FIG. 57. Right tibia of *Thrinaxodon*, SAM K. 1395, in A, anterior; B, posterior; C, medial; D, lateral views. X2. Abbreviations as in FIG. 56.

rounded part of the shaft (Figs. 56C, 57D). Distally the separation of flexor and extensor surfaces is more sharply defined.

The flexor surface is more or less straight from end to end but is convex mediolaterally. A deep, longitudinal groove is incised in the lateral side of middle of the shaft (*gr 2*, Figs. 56B,C, 57B,D). This groove, undoubtedly representing a muscular attachment, extends farther proximally than distally and is deepest at about the shaft midpoint. The groove is relatively longer and deeper in galesaurids than in larger cynodonts.

The distal end of the tibia is terminated by a flat, oval facet at right angles to the shaft axis. In the best preserved specimens this facet appears to be slightly convex although the articular cartilage may have formed a surface of somewhat different curvature. The apparent presence of apposing convex surfaces in the cynodont ankle joint (the other being the bulbous astragalar facet) is a peculiarity not easily explained.

FIBULA (Figs. 58, 59)

MATERIAL. Fibulae are the least well known of cynodont long bones. With very slender shafts and poorly ossified extremities they are usually disarticulated and damaged. Disassociated fibulae of *Cynognathus* and *Diademodon* are known from two collections (BPI 1675; NMB C.2701). A fibula (DMSW R.190), probably but not certainly referable to *Diademodon*, is one of the very few specimens associated with a tibia (DMSW R.189) from the same individual. Seeley (1895b: 148) described a fibula referable to *Tribolodon frerensis.* This specimen could not be located and Seeley's description and figure are inadequate for purposes of comparison. *Thrinaxodon* fibulae are preserved in BPI 287, BPI 376, NMB C.373, but only in SAM K.1395 are they completely freed of matrix.

The BPI 1675 collection, in which both *Diademodon* and *Cynognathus* are represented, preserves two types of fibulae which differ in a number of features. Since these fibulae are of approximately the same size the differences are probably not due to ossification but may be generically related. If so, this is a unique occurrence of major dissimilarity in the postcranial skeleton of these two genera (insofar as known). Of course it is still not possible to identify generically the fibular types. For convenience they are referred to as fibular type I and type II (BPI 1675).

The orientation of cynodont fibulae will remain in doubt until more complete, articulated material is recovered. Only SAM K.1395 preserves the tibia and fibula in what is probably an approximation of their true positions relative to each other (Fig. 59). Typically, however, this *Thrinaxodon* fibula is poorly ossified and cannot be compared with absolute certainty to those of larger cynodonts. The cynodont fibula is very much modified from the pelycosaurian fibula, unlike other limb bones, and therefore comparison between the two establishes nothing in terms of orientation.

MORPHOLOGY. The slender fibular shaft is slightly expanded at each end and bowed laterally. The proximal end with the articular facet for the femur is usually poorly ossified but may be reconstructed from DMSW R.190 and DMSW R.192. The articular facet for the humerus appears to have been round and a little convex. As preserved in these specimens it faces medially and slightly dorsally. From the adjoining surface of the proximal end a prominent flange projects posteriorly (*fi fl*, reconstructed in Fig. 58C,D). This flange may have taken part in the femoro-tibial articulation but more probably served as a musculotendinous process. Presumably the flange is homologous with the greatly expanded head of the monotreme fibula to which attaches part of the gastrocnemius, popliteus, flexor fibularis, tibialis posterior, flexor tibialis and peroneus longus muscles (Lewis, 1963). However, the unusual size and extensive muscular relations of the fibular head in monotremes is no doubt a specialization.

The shaft at the proximal end is three-sided and thus triangular in cross-section. A sharp ridge descends from the proximal end along the medial aspect (*m r*, Fig. 58C). In some specimens (type I, BPI 1675) the ridge terminates between the first and second quarters of the shaft, as in Figure 58C, while in others (type II) it is continuous with a ridge along the posteromedial aspect of the shaft. This represents a major difference between the two fibulae because in type I the ridge extends toward, but does not reach, another longer ridge along the anteromedial aspect of the shaft (*a r*, Fig. 58C), whereas in type II it is continuous with a second ridge (also present on type I, *pm r*, Fig. 58C) along the posteromedial aspect.

The medial surface of the shaft, narrow proximally, gradually widens distally (Fig. 58C). The distal part is flat, with a slight longitudinal convexity just below the shaft midpoint. The flat area is bounded by two long ridges (*a r*, *pm r* mentioned above). The more prominent anteromedial ridge reaches the distal end of the bone (Fig. 58A) and in type I is split near its proximal end (Fig. 58C). In type II the anteromedial

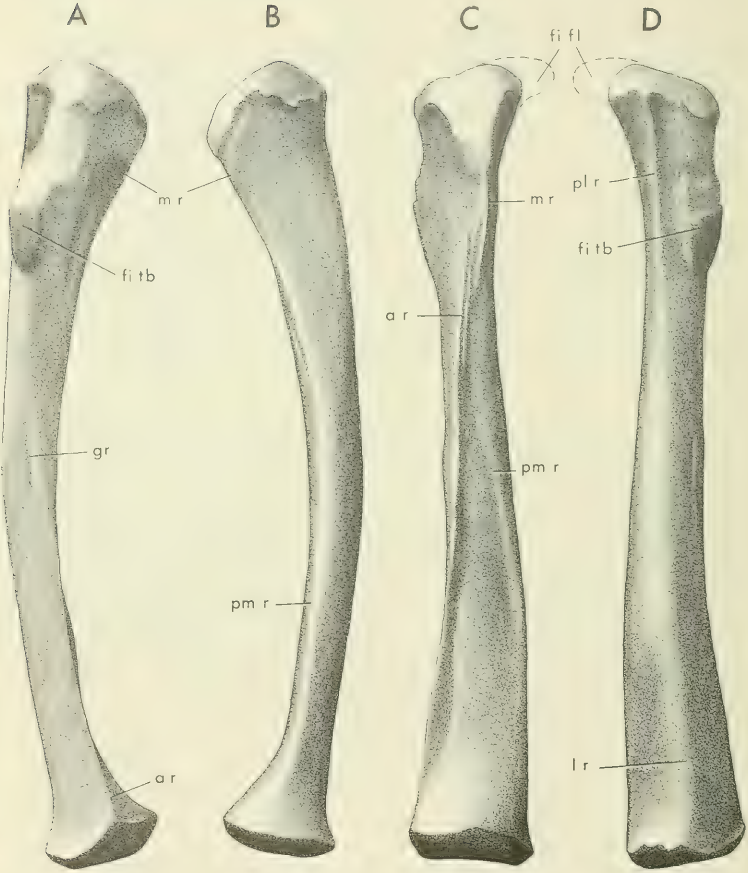
A
B
C
D
fi fl
m r
m r
fi tb
gr
a r
pm r
m r
a r
pm r
pl r
fi tb
l r

FIG. 58. Right fibula of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, in A, anterior; B, posterior; C, medial; D, lateral views. X1. Outline of proximal end reconstructed from DMSW R. 190 and DMSW R. 191. Abbreviations: *a r*, anteromedial ridge; *fi fl*, fibular flange; *fi tb*, fibular tubercle; *gr*, groove of unknown function; *l r*, lateral ridge; *m r*, medial ridge; *pl r*, posterolateral ridge; *pm r*, posteromedial ridge.

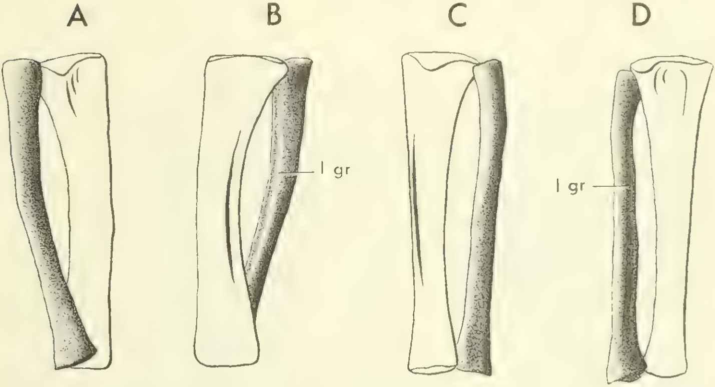

FIG. 59. Right fibula of *Thrinaxodon*, SAM K. 1395, associated with a tibia. A, anterior; B, posterior; C, lateral; D, medial views. X1. Abbreviations: *l gr*, groove presumed to be homologous with the space between *a r* and *pm r* in FIG. 58.

ridge also reaches the distal end of the shaft but bears a prominent flange in place of the split in the proximal end. The posteromedial ridge is less prominent and does not reach the distal end of the shaft in either type I (Fig. 58B) or type II.

In *Thrinaxodon* (Fig. 59) none of the foregoing features can be identified with certainty because of poor ossification. However, the medial surface of the shaft is incised by a longitudinal groove bounded on either side by distinct ridges (*l gr*, Fig. 59B,D). These ridges may represent the anteromedial and posteromedial ridges on the fibulae of larger cynodonts. The shaft is bowed laterally as in larger cynodonts but no further comparisons can be confidently made on the basis of available material.

It was noted above that the proximal end of the fibular shaft in larger cynodonts was triangular in cross-section, the medial angle being formed by a ridge (*m r*). In type I the other two angles of the proximal shaft are occupied by a posterolateral ridge (*pl r*, Fig. 58D) and a large anterolateral tuberosity (*fi tb*, Fig. 58A,D). In type II the posterolateral ridge is comparable but the tuberosity is merely a short, low flange.

In both types I and II a shallow groove is incised in the middle of the shaft along its anterior aspect (*gr*, Fig. 58A).

The distal end of the shaft is also triangular in cross-section but the triangle is oriented differently from that of the proximal end. Two angles are defined by the anteromedial and posteromedial ridges described above (Fig. 58A,B) and the third occurs as a lateral ridge (*l r*, Fig. 58D) which is confined to the distal half of the shaft.

The distal articular surface of the fibula is invariably poorly ossified. In one specimen of *Thrinaxodon* (SAM K.1395) and in type I the facet appears to be relatively flat. The former is oval in outline; the latter is piriform with its attenuated end beneath the terminus of the anteromedial ridge. It is unlikely that the distal end as preserved reveals much of the true shape of the articulating distal facet for tarsal contact.

PES (Figs. 60–62)

MATERIAL. The only complete pes available for study is that of an unidentified cynodont (BMNH TR.8) from the Middle Triassic Manda Formation of Tanzania. Associated with this specimen are a complete femur, most of the pelvis, and part of the lumbar series which displays ribs similar to *Cynognathus* and *Diademodon*. Cranial material preserved with this specimen indicates a generic assignment of either *Alcodon* or *Scalenodon* (A. W. Crompton, personal communication).

Various elements of the pes are known from *Thrinaxodon*. In BPI 376 the plantar aspect of the right pes is exposed, revealing an incomplete set of metapodials (but no mesopodials). Disarticulated tarsalia (SAM K.1395) are preserved with other *Thrinaxodon* specimens. Broom (1932b: 270) figured a complete *Thrinaxodon* pes but in such a diagrammatic manner that its accuracy is questionable. The specimen on which the figure was based is apparently lost. Invariably *Thrinaxodon* tarsal bones are poorly preserved and thus appear to be more dissimilar to the tarsals of larger cynodonts than they probably were in life.

Isolated ?tarsal (?carpal) elements of *Cynognathus* or *Diademodon* are preserved together in one collection (BPI 1675) but are not sufficiently numerous or distinct to make generic separation possible. None of the readily recognizable tarsal bones (calcaneum, astragalus) are present. Apparently this limited sample contains only distal tarsal elements, as well as distal carpal elements.

The pes associated with an almost complete skeleton of *Diademodon* sp. (USNM 23352) is composed of rather poorly preserved bone in hard, tenacious matrix. Complete preparation is therefore impossible without further damage to the specimen. A sufficient amount is exposed to show that in all dimensions the hindfoot was considerably smaller than the forefoot (compare Fig. 34A with 34B), a feature which is probably related to the disproportionately large size of the head (see Brink, 1955: fig. 7). Brink's reconstruction of this genus incorrectly depicts the hindfoot as being slightly larger than the forefoot which is a common condition among terrestrial tetrapods.

Finally, there is an excellently preserved, isolated calcaneum (DMSW R.191) of an unidentified cynodont; according to the D.M.S. Watson catalogue it is probably referable to *Diademodon* sp. The specimen has been cleared of matrix and reveals details not seen elsewhere.

The following description of the cynodont pes is based primarily on the Manda cynodont (BMNH TR.8).

MORPHOLOGY. The cynodont calcaneum is distoproximally elongate and dorsoventrally compressed (Figs. 60A,C,D, 61). In lateral view its outline is arched, being slightly concave ventrally and convex dorsally (Fig. 61C,D). A prominent, rugose tuber calcis (*tb c*) composes almost one-third the length of the bone and is directed posteroventrally. Much of the remaining anterior two-thirds of the dorsal surface is flat except that the lateral margin is reflected dorsally (Fig. 61A). In DMSW R.191 a shallow sulcus crosses the dorsal surface obliquely from the anteromedial edge (*s'*, Fig. 61A).

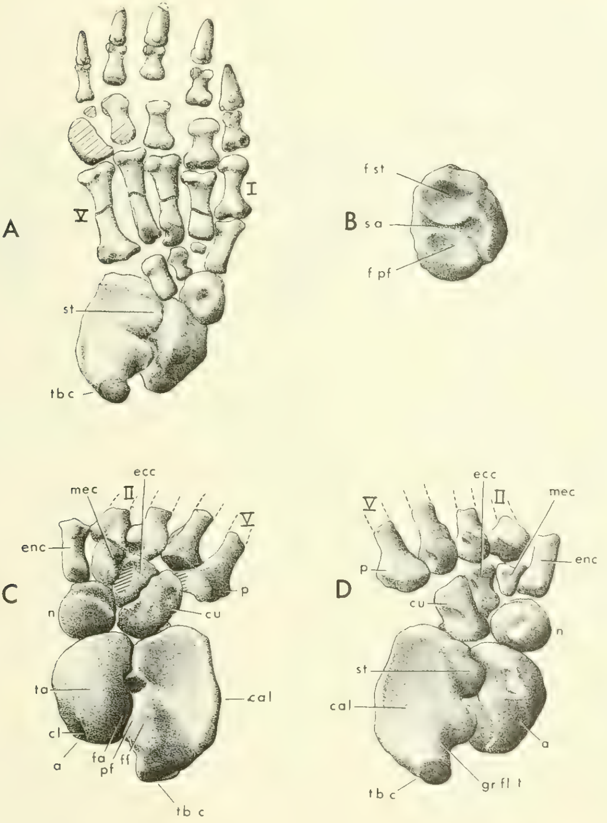

FIG. 60. Right pes of a Middle Triassic cynodont, BMNH TR.8, possibly referable to ?*Aleodon* or ?*Scalenodon*. A, plantar view of complete pes in situ, X1.2. B, ventrolateral view of the astragalus to show the two facets for articulation with the calcaneum, X1.6. C,D, dorsal and ventral views of the tarsus after further preparation, approx. X1.6; the calcaneum and astragalus have been reset to their correct positions relative to each other, but the other tarsals and metatarsal heads remain as found. Abbreviations: Roman numerals designate metatarsals; *a*, astragalus; *cal*, calcaneum; *cl*, cleft in astragalus of unknown function; *cu*, cuboid; *ecc*, ectocuneiform; *enc*, entocuneiform; *fa*, fibular facet of the astragalus; *ff*, fibular facet of the calcaneum; *f pf*, astragalar facet for the proximal calcaneal facet; *f st*, astragalar facet for the sustentaculum tali; *gr fl t*, groove for flexor tendon(s); *mec*, mesocuneiform; *n*, navicular; *p*, lateral process of metatarsal V possibly for insertion of short flexor and peroneal musculature; *pf*, proximal astragalar facet on the calcaneus; *s a*, astragalar sulcus; *st*, sustentaculum tali; *ta*, astragalar facet for the tibia; *tb c*, tuber calcis.

On the medial side of the calcaneum is a stout process that in dorsal view (Fig. 61A) appears rectangular in outline. The process lies almost entirely proximal (or posterior) to the transverse midline of the calcaneum. The process represents two separate articulations, one for the fibula (*ff*), the other for the astragalus (*pf*), but the delineation of the exact limits of the fibular facet is somewhat problematical. As here interpreted the fibula contacted at least the dorsal extremity of the rectangular process which has an oval, flat top (*ff*, Fig. 61A,D, Fig. 62B). The fibula may have also contacted part of the surface medially adjacent. This surface, which is rectangular in outline, bears one of the two calcaneal facets for the astragalus (*pf*, Figs. 61A, 62B). The orientation of this surface is dorsomedial (Fig. 61E). In BMNH TR.8 the medial process on the calcaneum does not project as far dorsally as in DMSW R.191, nor is the oval, dorsal extremity (*ff*) as clearly differentiated from the medially inclined surface (*pf*, Fig. 60C).

Anteroventral to the rectangular process is another process, the sustentaculum tali, which lies beneath the anterolateral aspect of the astragalus (*st*, Figs. 60A,D, 61A,B, D,E, Fig. 62B). This process represents an incipient morphological reorientation of the two proximal tarsals toward the mammalian condition in which the astragalus is supported by the calcaneum (see below). The rectangular process and the sustentaculum tali are separated by a sulcus (*s''*, Fig. 61D), evidently homologous with the intratarsal notch in pelycosaurs which Romer and Price (1940: 165) believed was for a "perforating artery". In DMSW R.191 the sulcus is more or less continuous with a previously described sulcus running obliquely across the dorsal surface (*s'*, Fig. 61A) and another sulcus extending for a short distance on the ventral surface (*s'''*, Fig. 61B).

On the medial side of the calcaneum between the rectangular process and the tuber calcis is a distinct groove for passage of a long flexor tendon (*gr fl t*, Fig. 60D). In DMSW R.191 the groove is apparently doubled by the occurrence of a low, dividing ridge (*gr fl t*, Fig. 61D).

In *Thrinaxodon* the calcaneum is oval by virtue of the fact that the tuber calcis was cartilaginous or not yet developed. The sulcus between the sustentaculum tali and rectangular process is distinct, but the processes themselves were apparently not ossified and are indicated only by indistinct tuberosities on the medial aspect of the calcaneum.

The astragalus is hemispherical with its flat surface directed ventrolaterally. On the anterior half of this surface is a large, oval facet for the sustentaculum tali (*f st*, Fig. 60B); posteriorly is a somewhat smaller, oval facet for the ventral half of the rectangular process of the calcaneum (*f pf*, Fig. 60B). The two facets are separated by a sulcus which represents the astragalar half of the tarsal sinus (*s a*, Fig. 60B). The dorsomedial half of the astragalus is bulbously convex (Fig. 60C) and the crural facets are not well preserved. The fibular facet is apparently represented by a small, flat surface on the posterolateral aspect of the convexity (*fa*, Fig. 60C) lying opposite the fibular facet on the calcaneum. A V-shaped notch is thus formed to receive the distal end of the fibula. The location of the tibial facet is more conjectural. There is no clearly defined facet on the dorsal surface of the astragalus which might represent the tibial contact. The most likely possibility is that the tibia articulated with the entire bulbous dorsal surface of the astragalus (*ta*, Fig. 60C). Since the crus is not preserved with these proximal tarsals there is no means of estimating how much of the dorsal surface was involved. The only noticeable feature on the dorsal aspect of the astragalus is a

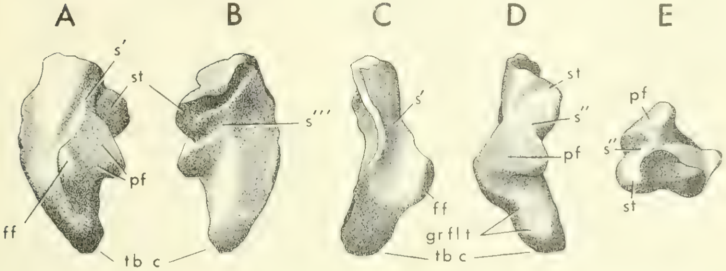

FIG. 61. Left calcaneum of a cynodont, DMSW R.191, possibly referable to *Diademodon*, in A, dorsal; B, ventral; C, lateral; D, medial; E, distal views. X1. Abbreviations as in FIG. 60 except: s', s'', s''', dorsal, medial and ventral parts, respectively, of a continuous calcaneal sulcus.

posteromedially located cleft of uncertain function (*cl*, Fig. 60C). An astragalus of *Thrinaxodon* also possesses this feature and is otherwise similar in form to that of the Manda cynodont.

The navicular is irregularly oval and bears a slight depression on its plantar surface (*n*, Fig. 60D). Its articular surface for the astragalus is shallowly concave. In addition to the astragalar contact it articulates with the first, second and third distal tarsalia (ento-, meso- and ectocuneiforms), and probably with the fourth distal tarsal (cuboid) as well. The nature and extent of these articulations is not certain because there has been some post-mortem displacement and because the articulating surfaces are not well preserved. Thus in Figure 60C and D the calcaneum and astragalus have been replaced in the correct position relative to each other but the navicular and distal tarsalia remain in approximately the same position in which they were found (Fig. 60A).

There are four distal tarsalia (Fig. 60C,D). The most medial (entocuneiform) is almost perfectly rectangular although its dorsal aspect is somewhat narrower than its ventral aspect. Distally it articulates with metatarsal I and apparently with a corner of metatarsal II. The second distal tarsal (mesocuneiform), the smallest of the tarsalia, is wedge-shaped by virtue of having a larger dorsal than ventral surface. Distally it articulates with metatarsal II; apparently it was accommodated medially and laterally by slight recesses in the adjacent distal tarsalia (I and III). Proximally it has only a short contact with the navicular. The third distal tarsal (ectocuneiform) is somewhat 8-shaped in outline, articulating distally with metatarsals III and possibly IV. The fourth distal tarsal (cuboid) is larger than the entocuneiform but has a rather similar rectangular shape. Distally it articulates with metatarsals IV and V, laterally with the ectocuneiform and navicular, and proximally with the astragalus and calcaneum. Like the other distal tarsals both the ectocuneiform and cuboid are wedged-shaped; they have broader dorsal than ventral surfaces (cf. Fig. 60C and D).

A complete set of metatarsals is known only from the pes of the unidentified Manda cynodont (BMNH TR.8). In this specimen the shaft diameters are all approximately the same, the greatest variability being in the shaft lengths and in the form of the proximal ends. The distoproximal lengths in millimeters are: I, 8.4; II, 10.2; III, 13.2; IV, 13.8; V, 14.6. The proximal ends of metatarsals I and II are mediolaterally expanded and bear rather symmetrical, trochlea-like articular surfaces. The proximal ends of III and IV, however, are mediolaterally compressed. Their articular surfaces are bulbous and are excavated laterally to permit articulation with the next (lateral) metatarsal (Fig. 60D). The proximal end of metacarpal V is mediolaterally expanded and bears a flat articular facet for the cuboid on its medial side. Laterally is a process (*p*, Fig. 60C,D) similar to that in many mammals where short flexor and peroneal musculature may have inserted. The distal ends of all of the metatarsals are similarly constructed; each is a trochlea-like facet with a vertical, median groove (Fig. 60A).

The digital formula of the Manda pes (BMNH TR.8) is 2-3-3-3-3. Broom (1932b: fig. 91) figured a *Thrinaxodon* pes having a count of 2-3-4-5-3 with the second phalanx of digit III and the second and third phalanges of digit IV reduced to intercalated discs. However, another pes of *Thrinaxodon* (BPI 376), in which the third and part of the fourth digit have been exposed, shows no trace of vestigial phalanges such as Broom figured. It is possible that they were lost post-mortem or during preparation but this in unlikely considering the pes is nearly articulated and the black bone is readily distinguished from the light-colored matrix. In view of Broom's unreliable interpretations of digital formulae in the carpus of *Thrinaxodon* and *Leavachia* (see above, p. 129 ff.) his statements concerning the pes are also suspect—especially because his figured specimen is apparently lost. While the question of pedal digital formulae in earlier cynodonts must remain open there is no doubt that the later forms attained the mammalian number.

The proximal phalanges are short and dumbbell-shaped with a rather sharp, median constriction. Their proximal articular surfaces are rectangular and vertical, their distal surfaces hemicircular and oblique to the vertical plane. The exception is the distal articular facet of the first proximal phalanx, which is unexpanded and bears a simple trochlea to accommodate the claw-bearing ungual phalanx. With a limited sample of proximal pedal phalanges known, there are no obvious morphological features, except relative size, which distinguish pedal from manual proximal phalanges.

The four penultimate phalanges are also indistinguishable from their analogues in the manus. The proximal articular facet is approximately rectangular and somewhat convex; the distal facet forms a trochlea for the ungual phalanx. There is a distinct morphological gradation from penultimate phalanx II which is robust and distinctly expanded at each end to that of V which is slender and very little expanded.

The ungual phalanges of BMNH TR.8 are dorsoventrally compressed and only slightly recurved. In the former respect they are different from other cynodont unguals which are more rounded and cone-like. Furthermore they are rather blunt—certainly not as sharply pointed as other cynodont unguals. This feature, however, could very well be a specialization of this unknown genus rather than a general cynodont character. The typical tuberosities for insertion of a long digital flexor tendon are present on the proximoventral aspect of each ungual.

3. FUNCTIONAL CONSIDERATIONS OF THE PES

Cruro-Pedal Joint

A discussion of the evolution of the mammalian cruro-pedal joint may conveniently begin with the pelycosaur tarsus which is sufficiently primitive to bear resemblance to the captorhinomorph pattern (Schaeffer, 1941b: 448-449). Romer and Price (1940) described the pelycosaur tarsus in detail and Schaeffer (1941b) discussed the pelycosaur tarsus in terms of function. Schaeffer stated that his functional interpretation is drawn largely from Romer's work but since no such detailed analysis can be found in Romer and Price's *Review of the Pelycosauria* the conclusions must be regarded as Schaeffer's. Schaeffer concluded that the long axis of the pelycosaur foot was directed forward during locomotion and that initially the body weight was transferred to the ground by the calcaneum and astragalus. Subsequently the weight was shifted to the metatarsals as the posterior part of the foot was lifted off the ground. Such a functional system, according to Schaeffer, must have generated "tension-compression stresses of considerable magnitude" which were probably resisted by tarsal ligaments and associated musculature.

Schaeffer's interpretation is questionable only with regard to the orientation and functional role of the calcaneum and astragalus during the initial phase of each stride. An important feature to understanding hindlimb function is the nature of the cruro-pedal joint. Opposing articular surfaces of this joint in pelycosaurs are more or less flat; movement here was probably a limited range of flexion and extension. In order for locomotory forces to have been transmitted by the calcaneum and astragalus (even via a heel pad as Schaeffer suggests) and not by the more distal tarsals, the calcaneum and astragalus must have been close to and nearly parallel with the ground. Yet cruro-pedal joint movement was probably so limited that the crus would have also assumed a similar orientation. In such a posture the muscular effort to raise the crus (and thus initiate the propulsive phase of the stride) would tend to disarticulate the cruro-pedal joint because the forces would be directed parallel to the plane of the articular surfaces. In fact the cruro-pedal joint appears to be adapted to transmit forces largely perpendicular to its articular surfaces. For this reason the pelycosaur calcaneum and astragalus probably did not have a plantar contact during the initial phase of propulsion, but remained off the ground throughout the entire stride (Fig. 51A).

Schaeffer's contention that the pelycosaurian tarsus was subject to considerable stress during locomotion is important to understanding subsequent developments in therapsid and mammalian cruro-pedal joints. The weight borne by the hindfoot was transmitted from the crus to the distal tarsus and metatarsus via the astragalus and calcaneum. The tarsus and metatarsus formed an arc (concave forward) between the horizontal digits and the crus (lateral view, Fig. 51A). At the end of a step, with the crus in a vertical or near vertical position, the arc was most pronounced and the tendency to intertarsal dislocation greatest. As Schaeffer suggested, this inherent weakness must have been offset by strong tarsal ligaments and muscles. However, the presence of strong ligaments must have also restricted the mobility of the pes to a limited range of flexion and extension.

Schaeffer (1941b: 449) stated that "not until the mammalian stage was reached, was a longitudinal tarsal arch created to counteract the stresses". This statement might be interpreted to mean that there was little or no functional evolution of the therapsid pes beyond the pelycosaurian condition. To the contrary, Schaeffer's studies (1941a, b) provide ample evidence of mammalian pedal features among therapsids. Of particular importance is the development of the plantigrade pes. Strictly defined, plantigrade posture is contact of the entire sole with the ground. In mammals a plantigrade posture involves plantar contact of the skin immediately beneath the calcaneal tuber. Among therapsids, however, the plantar surface of both the calcaneum and astragalus participated in support of the heel. Ultimately complete astragalar superposition removed the astragalus from plantar contact, thus creating a mammalian type of plantigrade foot (see below, p. 200). Derivation of a therapsid type of plantigrady from the pelycosaurian posture in which neither calcaneum nor astragalus had plantar contact involved: 1) distal displacement of the fibulo-tarsal articulation onto the dorsum of the calcaneum and astragalus and 2) lateral displacement of the tibio-astragalar articulation onto the dorsum of the astragalus. Displacement of the latter articulation is a trend begun among pelycosaurs and continued among therapsids (Schaeffer, 1941b: 449); in gorgonopsids of the lower *Tapinocephalus* zone both the fibular and tibial facets are already on the dorsum of the calcaneum and astragalus, respectively (Boonstra, 1965). The pes of a cynodont from the Manda Beds (BMNH TR.8) retains the dorsal cruro-pedal articulation developed among earlier therapsids. The functional significance of therapsid platigrady appears to relate to specialization of the cruro-pedal joint for increased flexion and extension. In pelycosaurs the intertarsal, tarso-metatarsal and metacarpo-phalangeal joints probably all participated in pedal flexion and extension but were limited in their individual contribution to movement by ligaments. These ligaments, as suggested above, would have been necessary to reinforce the arcuate arrangement of foot bones (see lateral view, Fig. 51A) against bending moments generated by body weight and propulsive force. The relatively flat cruro-pedal articular surfaces are evidence that flexion and extension here were probably not much greater than at the intertarsal joints. The elevated posture of the proximal tarsus and the relatively small articular surfaces of the cruro-pedal joints almost certainly necessitated supporting ligaments that in turn restricted joint motion. In therapsids the plantar contact of the calcaneum and astragalus provided extrinsic stability to the proximal tarsus as the cruro-pedal joint became specialized for an increased range of flexion and extension. Concomitantly, the remaining tarsals no longer participated individually in flexion and extension but became functionally conjoined with the proximal tarsals to form a lever powered largely by the triceps surae. Specialization for this movement is further developed in mammals. The malleoli and their associated ligaments are major stabilizing features of the mammalian ankle joint, but malleoli are as yet unknown in any cynodont. The evolution of a plantigrade posture therefore appears to be a principal factor in stabilizing an increasingly mobile ankle joint that was evolving as part of a triceps surae-calcaneal tuber lever system.

TARSUS

The acid-prepared calcaneum and astragalus of BMNH TR.8 reveal several important features not previously known in cynodonts. These features represent incipient specializations toward a mammalian type of calcaneum and astragalus. First, the calcaneum is anteroposteriorly elongate, thus approaching the characteristic mammalian shape. Approximately half of its width is composed of a thin, lateral flange, the outline of which (seen in dorsal view, Fig. 62B) is straighter from front to back than that in primitive *Tapinocephalus* zone therapsids (see Boonstra, 1965 and 1966); the flange is apparently in the process of reduction. Its absence would result in proportions essentially similar to that of a mammalian calcaneum, although some mammals (e.g., *Didelphis*) retain a slight lateral shelf on the calcaneum.

A second important feature is the nature of the articulation between the astragalus and calcaneum. The two facets on the calcaneum (*st, pf*) are so aligned as to represent different parts of a single convexity which is divided by a calcaneal sulcus (*s″*, Fig. 61D). The opposing astragalar facets represent parts of a single concavity also divided by an astragalar sulcus (*s a*, Fig. 60B). Therefore the calcaneo-astragalar articulation is a shallow ball and socket joint with the possibility of more than the inversion-eversion movements that characterize this joint in mammals. More important than the intertarsal movement, however, is the support afforded by the calcaneum for the astragalus, for the astragalus actually overlaps the calcaneum. Although the opposing facets meet at angles of about 45° to the horizontal with the resultant tendency for the astragalus to dislocate medially, ligaments probably reinforced the articulation. The astragalus appears to have been supported as much by the calcaneum as by its own plantar surface. As a result, the plantar surface of the astragalus is reduced to a rather narrow surface in close proximity to the plantar surface of the calcaneum (Fig. 60D). This condition represents a stage in the evolution of the mammalian type calcaneo-astragalar joint in which the astragalus no longer has a plantar contact but is supported entirely by the calcaneum.

Schaeffer (1941a: 6) claimed that the pes of *Bauria cynops* (AMNH 5622) more closely approximates the mammalian condition than that of any other known therapsid and Romer (1956: 404) expressed a similar view. Schaeffer implied that the following characteristics of the bauriamorph tarsus are significantly mammal-like: the degree of "consolidation" or interlocking of tarsal bones, a "true, but weakly developed head" on the astragalus, and a transverse tarsal arch as indicated by a cuboideonavicular ligament, a wedge-shaped mesocuneiform (centrale 2) and a rudimentary sustentacular process. The cynodont tarsal material available to Schaeffer was inadequate, as his brief account (1941b: 454) testified. Now that more satisfactory material is known, a comparison of the supposedly advanced bauriamorph tarsus with that of cynodonts is possible.

Schaeffer's first criterion of comparison—"consolidation" or interlocking of tarsal bones—is unquestionably characteristic of mammalian tarsi. However as a criterion for estimating the degree to which a synapsid tarsus approached a mammalian pattern, "consolidation" is a vague and subjective standard. As Schaeffer realized, specific intertarsal relationships are the most meaningful features for evaluating the evolution of a functionally mammalian tarsus. Furthermore, some intertarsal articulations in fossil and living reptiles are comparable in complexity to those in mammals. The apparent simplicity of some fossil reptilian tarsi may be largely the result of non-preservation of cartilage. Therefore no attempt will be made to evaluate the "consolidation" of the bauriamorph and cynodont tarsus; instead, specific intertarsal relationships will be considered.

ASTRAGALAR SUPERPOSITION

The calcaneo-astragalar articulation will be considered first as it represents one of the most important differences between the reptilian and mammalian tarsus. In mammals the astragalus lies between the calcaneum and the crus and has no plantar contact. From the reptilian position medial to the calcaneum the astragalus has moved laterally and dorsally to override and to be supported by the calcaneum. On the calcaneum of *Bauria* (AMNH 5622) there is a very small sustentacular process which extends beneath the astragalus. The calcaneal support of the astragalus was therefore incipient, but the astragalus in AMNH 5622 is apparently preserved in its correct position and lies almost entirely medial to the calcaneum as in reptiles. Calcaneal support of the astragalus in *Bauria* represents only a slight shift in weight distribution over the condition in primitive therapsids and pelycosaurs. Schaeffer (1941a: 4) stated that the calcaneo-astragalar articulation is "weak, as the articular facets of the related bones are narrow, plain surfaces." The calcaneo-astragalar articulation in cynodonts is more extensive than that in *Bauria*. The anteroposterior length of the sustentacular process approaches 30 percent of the calcaneal length in BMNH TR.8 which is comparable to mammalian proportions; in *Bauria* the length is about 20 percent. Secondly, the calcaneo-astragalar contact is almost as extensive as the plantar surface of the astragalus, evidence that much of the astragalar support was transferred to the calcaneum. The functional association of these tarsal bones is evident in Figure 60C and D and represents an advance over the narrow calcaneo-astragalar contact of bauriamorphs.

The evolution of the mammalian calcaneo-astragalar, or sub-talar, joint is illustrated diagrammatically in Figure 62. In pelycosaurs there are four features on the medial side of the calcaneum which are recognizable among cynodonts. On the distal end of the medial side there is a small articular facet on the astragalus (*st*, Fig. 62A). This calcaneal facet is continuous distally, at least as an osteological feature, with the calcaneal facets for the cuboid and fifth distal tarsal. Proximally this facet is separated from another facet (*pf*, Fig. 62A) for the astragalus by the intervening calcaneal sulcus (*cs*, Fig. 62A). The calcaneal sulcus is opposed by a similar astragalar sulcus, thus constituting a foramen. The proximal facet is confluent with a third and still more proximal facet (*ff*, Fig. 62A) which represents half of the articular surface for the fibula. Thus along the medial edge of the calcaneum there occur three facets and one sulcus. The two pairs of calcaneo-astragalar facets are quite flat and are evenly matched in

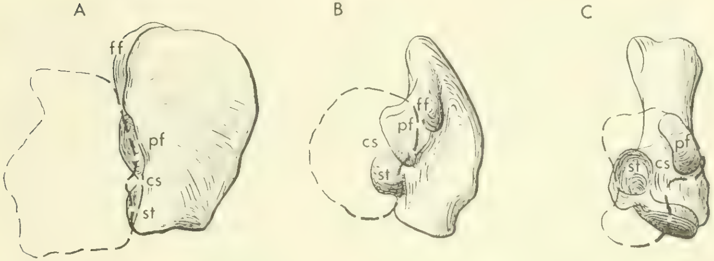

FIG. 62. Proximal tarsals of A, a pelycosaur (anterior view); B, a cynodont (dorsal view); C, a mammal (dorsal view). Astragalus outlined by dashed line; *cs*, calcaneal sulcus; *ff*, facet for fibular articulation; *pf*, proximal facet for astragalus; *st*, sustentacular facet, or its homologue, for astragalar articulation. Not to scale.

size; therefore, there could have been only a limited degree of movement between the astragalus and calcaneum. Furthermore, any substantial movement between these two tarsals would disrupt the fibular articulation which could be maintained only by a constant calcaneo-astragalar relationship.

In cynodonts (Fig. 62B) the same four features occur in linear sequence as in pelycosaurs although their orientation and position on the calcaneum is shifted. The distal facet (*st*) no longer faces medially, but is oriented dorsally and medially. This facet is supported by a sustentaculum tali which protrudes as a distinct process beneath the overlying astragalus. The calcaneal sulcus (*cs*) obliquely crosses the medial edge of the calcaneum. The proximal facet for the astragalus (*pf*) does not shift position as much as it changes orientation; like the sustentacular facet it faces dorsally as well as medially so as to support the astragalus from below. The fibular facet (*ff*) on the calcaneum displaces to the lateral side of the proximal astragalar facet; the primitive position of the fibular facet is now occupied by the tuber calcis. These modifications all relate to the calcaneal support of the astragalus. The more dorsal orientation of the astragalar facets on the calcaneum permit the astragalus to be partially supported by the calcaneum. The functional significance of astragalar superposition is discussed by Schaeffer (1941b: 455–457) and other authors cited by him. In simplest terms, superposition united the astragalus, which primitively transmitted most of the weight via the tibia, with the calcaneum; the calcaneum, through the development of a tuber, permitted the foot to function as a lever powered by triceps surae musculature and thus enhanced locomotory efficiency. With the growth of the tuber and the development of a plantigrade pes, the fibular facet is displaced from its primitive position at the proximomedial corner of the calcaneum.

In mammals (Fig. 62C) the trends evident among cynodonts are developed further. The sustentaculum tali and its astragalar facet (*st*) occur in the same position; the sustentaculum is a more robust feature. The proximal facet for the astragalus (*pf*) migrates further laterally and distally, and thus the astragalus loses any plantar contact of its own. The calcaneal sulcus (*cs*) which separates the two facets now runs obliquely across the dorsum of the bone instead of across its medial edge as in cynodonts and pelycosaurs. The fibular facet tends to be transferred to the astragalus as a result of the narrowing of the calcaneum and the further reduction of the weight-bearing role of the fibula. The fact that the two astragalar facets on the calcaneum (*st, pf*) come to lie in a mediolateral relationship, contrasting to the proximodistal relationship in pelycosaurs, is probably related to the necessity for stabilizing the calcaneo-astragalar joint. Had astragalar superposition occurred by an equal amount of lateral migration on the part of both the sustentacular (*st*) and proximal (*pf*) facets, the sustentacular facet would lie directly distal to the proximal facet. Such an arrangement would obviously be prone to medial and lateral dislocation. In mammals the form of the calcaneo-astragalar joint tends to prevent such dislocation, despite the fact that the astragalus is supported only by a comparatively narrow calcaneum. First, the facets are in a mediolateral relationship, and second, their respective facet surfaces are inclined toward the midaxial line of the calcaneum. Both features tend to prevent the astragalus from dislocating to the medial or lateral side of the calcaneum.

During the pelycosaur-mammal transition the calcaneo-astragalar foramen apparently was modified for an entirely different function. In the tarsus of pelycosaurs and other primitive forms the foramen is formed by opposing grooves in the calcaneum (*cs*) and astragalus (Fig. 62A). Since neither bone is very thick, the foramen thus formed is only a short canal. Functionally, the foramen is usually regarded as representing the passage of a perforating artery (Romer and Price, 1940: 163; Schaeffer, 1941b: 430; Romer, 1956: 392), although no author cites evidence for a homologous structure in any living reptile. Whether arterial or venous, a vascular function for the foramen would seem to be indicated by the occurrence of sulci leading from both the dorsal and ventral openings in various pelycosaurs. The sulci are also present in cynodonts. Furthermore, well-preserved calcanei and astragali of pelycosaurs show that opposing grooves are evenly rounded, forming an almost perfectly circular foramen or sinus—a feature common to vascular or neurovascular foramina. There is no reason to doubt that the calcaneo-astragalar sinus of cynodonts is homologous with the foramen of pelycosaurs, for the sinus is bounded by the same two calcaneo-astragalar articulations which have only slightly shifted from their primitive position. However, the cynodont sinus is relatively longer than in pelycosaurs. In mammals the same two calcaneo-astragalar articulations are retained but their repositioning causes the sinus to run obliquely across the dorsum of the calcaneum. But more important, however, is the fact that in mammals there is no major vascular or nerve trunk traversing this sinus. Instead, the tarsal sinus is occupied primarily by a robust calcaneo-astragalar interosseous ligament, and secondarily by small neurovascular structures supplying the ligament and bone. This ligament is continuous distally and proximally with other cruro-pedal joint ligaments and serves the obvious function of reinforcing the calcaneo-astragalar joint from within. The vascular foramen of pelycosaurs thus appears to have been retained in mammals to meet mechanical rather than vascular requirements. The development of independent movement of the calcaneum and astragalus is likely to have introduced interference to the major vascular or neurovascular bundle passing in such close proximity to an active joint. With the course of this bundle transferred elsewhere, the sinus, filled with connective tissue, assumed a new function. A strong calcaneo-astragalar bond is necessitated by the fact that extension of the foot in locomotion is accomplished largely by muscular action on the calcaneum, whereas body weight is transferred to the calcaneum, and other tarsals, by the astragalus.

If the course of tarsal sinus evolution as outlined above is correct, then it would be of interest to know whether the cynodont tarsal sinus was vascular or ligamentous in function. Discrete sulci leading away from either side of the sinus (*s′*, *s‴*, Fig. 61A,B) opening are evidence that major vascular or neurovascular structures were still associated with the sinus. However, the walls of the sinus are asymmetric—not rounded as in a strictly vascular passage. The problem cannot be satisfactorily resolved without additional and better preserved material.

ASTRAGALO-NAVICULAR JOINT

A second characteristic feature of the mammalian tarsus is a rounded head on the astragalus that articulates with the navicular; the head proper is separated from the rest of the astragalus by a neck. Schaeffer (1941a: 4) claimed that the *Bauria* astragalus possesses a head but no neck, and implied thereby that this mammalian feature is incipiently differentiated. Reexamination of the specimen (AMNH 5622) reveals that Schaeffer's recognition of an astragalar head is difficult to justify. The anterior aspect of the astragalus articulates with the navicular and cuboid, contacting the former somewhat more extensively than the latter. In both cases the astragalar articular surface is slightly concave, not convex as is the astragalar head in mammals. The facets in *Bauria* are not borne on a process distinct from the astragalus, but occur flush with the main body of the bone. A "head", therefore, cannot be recognized. Neither can a head be recognized on the BMNH TR.8 astragalus. However, the navicular and cuboid facets on the astragalus of this cynodont appear to be flat or slightly convex and thus approximate the astragalar head of mammals more closely than that of *Bauria*.

TRANSVERSE TARSAL ARCH

One of the most characteristic features of a generalized mammalian pes is a transverse tarsal arch. In cross-section through the distal tarsus, the transverse arch is an arcuate arrangement of the wedge-shaped cuboid and three cuneiforms. The dorsal surfaces of these bones are larger than the plantar and thus adjacent bones act as keystones to form a dorsally bowed arch. The arch is maintained by joints, ligaments and muscular action; it serves the function of providing inherent structural strength while at the same time being sufficiently resilient to absorb shocks.

Schaeffer (1941a: 6) claimed that in *Bauria* "several features support the conclusion that there was a low transverse tarsal arch, namely, the indication of a well-developed cuboideo-navicular ligament, the wedge-shaped mesocuneiform, and possibly the rudimentary sustentacular process." The evidence for a strong cuboideo-navicular ligament is a knob-like process on the plantar surface of the cuboid. However, similar processes are common on the plantar surface of tarsals and may serve as points of tendon insertion or plantar support as well as intertarsal ligament attachment. The evidence for a cuboideo-navicular ligament is not conclusive. While such a ligament is probably necessary for a transverse arch, its presence is not sufficient to demonstrate the existence of a transverse arch. Neither can the incipient development of astragalar superposition be construed as evidence of a transverse arch. In fact the only certain evidence of a transverse arch are wedge-shaped tarsals which result in a "keystone" arch. In *Bauria* only the mesocuneiform is perceptibly wedge-shaped. If there were any arching effect it must have been low, as Schaeffer correctly concluded. In the Manda cynodont (BMNH TR.8), however, all the distal tarsals are more or less wedge-shaped. The cuboid, ecto- and mesocuneiform each have a dorsal surface which is larger than the plantar surface and thus each acts as a keystone. The morphology of the entocuneiform is reversed with a dorsal surface slightly narrower than the plantar surface. The reversed wedging heightens the arching effect of the cuneiforms because the entocuneiform surface articulating with the mesocuneiform is inclined dorsolaterally. An analogous condition is best known in the human foot in which the "reversed keystone" shape of the entocuneiform serves the same function. The cynodont pes is unquestionably further advanced than that of *Bauria* with regard to developing a mammalian transverse tarsal arch.

TARSO-METATARSAL JOINTS

A fourth important aspect of the mammalian tarsus is the arrangement of the four distal tarsalia into a compact row of ossicles. Complex intertarsal and tarso-metatarsal articulations, reinforced by strong ligaments, create a cohesive but resilient structure. Partly correlated with this feature are the extensive articulations formed between the proximal ends of adjacent metatarsals. Such reinforcement probably serves to distribute forces more evenly across the tarsus and relieve stresses which might otherwise be borne by a single metatarsal. Both features are correlated with the mammalian tendency to narrow the plantar surface of the foot. In contrast, the primitive reptilian condition, approximated among pelycosaurs, is characterized by a broad, arcuate arrangement of the full complement of five distal tarsals (Fig. 51A). The digits tend to be splayed, the first and fifth diverging at angles of 60° or more (see Romer and Price, 1940: fig. 41). The proximal ends of the metatarsals are transversely expanded and among many forms the proximolateral corner of one metatarsal may overlie the proximomedial corner of the next lateral metatarsal. This articulation is a simple overlap and only superficially approximates the extensive intermetacarpal joints of mammals. In such primitive therapsids as dinocephalians the pes is essentially pelycosaurian with regard to these features; intermetatarsal contacts are not developed and the fifth distal tarsal is retained (see Boonstra, 1966). In more advanced therapsids, e.g., gorgonopsids, the distal tarsalia are more consolidated and reduce to four in number. However, the digits retain the splayed arrangement and the intermetacarpal contacts are only incipiently developed (e.g., *Lycaenops*; see Colbert, 1948).

With regard to the same features the pes of BMNH TR.8 represents the closest known approximation to the mammalian condition. The distal row of tarsalia forms a compact arch in which the intertarsal articulations are complex and snugly fitted. The metatarsals and digits are sub-parallel, as in mammals, and are not divergent as in primitive synapsids. Most striking, however, are the complex articulations formed between the proximal ends of adjacent metatarsals. The proximomedial corner of the head of metatarsal V is received in a distinct groove on the proximolateral aspect of the metatarsal IV head (Fig. 60D). A similar pattern is repeated for metatarsals IV and III (Fig. 60C,D). The proximomedial side of the metatarsal II not only contacts metatarsal I but also the entocuneiform which is proximodistally elongate and extends farther distally than any other tarsal. This particular relationship is typical of mammals with a relatively generalized foot (e.g., *Didelphis*, *Taxidea*). The pes of *Bauria cynops* (AMNH 5622) is not sufficiently preserved or prepared to permit a confident determination of these details. It appears that the degree of proximal contact between metatarsals is less advanced than in BMNH TR.8. Furthermore, it is doubtful whether metatarsal II had as much contact with the entocuneiform as Schaeffer's reconstruction depicts. Whereas the cynodont pes definitely displays features that are recognizably mammalian, the bauriamorph pes as now known shows only the possibility that it may have closely approximated—but not attained—the cynodont level of organization.

CONCLUSIONS

No suite of postcranial features in the cynodont skeleton is so mammal-like as to constitute proof that mammals arose from known members of this group. Yet in many characters cynodonts are well advanced toward a mammalian pattern. Moreover, no known feature in the postcranial skeleton debars cynodonts from being the reptilian ancestors of mammals. Thus, the presence of many advanced, mammalian characters in the cynodont postcranial skeleton increases the probability that mammals were derived from a cynodont therapsid.

The principal conclusions of this study, aside from the descriptive text, may be summarized as follows:

1) The cynodont atlas-axis complex retains the same number of elements as in pelycosaurs and in reptiles generally. Morphologically, however, the cynodont pattern is incipiently specialized for atlanto-occipital flexion and extension and atlanto-axial rotation—the characteristic movements of the mammalian atlas-axis complex.

2) The evolution of the mammalian type of atlanto-occipital flexion and extension is characterized by i) a doubling of the condyles, ii) their subsequent displacement to the lateral margins of the foramen magnum, and iii) a migration of the foramen magnum from a position in the middle of the posterior aspect of the skull to a position on the posteroventral aspect. In all except the most primitive cynodonts the condyles are double. Condylar displacement to the mammalian position is incomplete, however, for they occur at the ventrolateral margins of the foramen magnum. The position of the foramen magnum is essentially mammalian. All of these changes are related to increasing the range of flexion-extension and concomitantly minimizing the resultant deformation of the spinal medulla.

3) The evolution of the mammalian type of atlanto-axial rotation involves i) development of a dens, or odontoid process, and transverse, apical and alar ligaments, ii) loss of atlanto-axial zygapophyses, and iii) enlargement of the atlanto-axial intervertebral foramen. The dens is not the exact homologue of the atlas centrum as is generally believed. The dens is a neomorphic addition to the atlas centrum and reinforces, together with its associated ligaments, the altanto-axial joint, acting as a functional substitute for the lost atlanto-axial zygapophyses. Zygapophyses tend to restrict intervertebral rotation and are lost at the mammalian atlanto-axial joint which is specialized for rotation. The enlargement of the atlanto-axial intervertebral foramen is related to the specialization of the atlanto-axial joint for rotation and the necessity for preventing occlusion of the traversing neurovascular structures during rotation. Cyno-

donts possess an incipient dens, reduced atlanto-axial zygapophyses, and an enlarged atlanto-axial intervertebral foramen. It is likely that cynodonts had acquired at least a limited ability to rotate the atlas and head on the axis.

4) The vertebral count of *Thrinaxodon* is seven cervicals, thirteen thoracics, seven lumbars, five sacrals and at least five caudals. In *Cynognathus* the count is the same except that there are fifteen thoracic vertebrae. The cervical series, already seven as in most mammals, is moderately well differentiated from the thoracic. The thoracic series is differentiated from the lumbar on the basis of rib morphology; otherwise the differences are gradational and are relatively small. In *Thrinaxodon*, at least, all thoracolumbar vertebrae posterior to the fourth thoracic bear anteroposteriorly elongate neural spines; the anterior edge of each spine is received in a vertical cleft in the posterior margin of the preceding spine. This arrangement restricted vertebral column extension and it is probable that cynodonts employed only a very moderate range of sagittal flexion and extension during locomotion, less than in most mammals. All vertebrae in *Thrinaxodon*, with the exception of the atlas and the posterior caudals, bear anapophyses. The five sacral vertebrae are not fused. The exact number of caudal vertebrae, not known in any cynodont, was probably small and hence cynodonts were comparatively short-tailed.

5) In *Thrinaxodon* all presacral ribs bear near the proximal end a flat, expanded costal plate which imbricates with adjacent costal plates. In the earliest known cynodonts no costal plates are present. In later forms such as *Cynognathus* costal plates are retained in the posterior thoracic and the lumbar regions and are lost or are vestigial elsewhere. Typically the lumbar and sacral ribs are fused to the vertebrae in those forms possessing costal plates. Costal plates served for the insertion of the ilio-costalis division of the epaxial musculature. The elaborate costal plates of the most advanced cynodonts were characterized by an interlocking device with two pairs of articular facets on each plate.

6) The imbrication of adjacent costal plates did not inhibit lateral flexure of the vertebral column. Costal plates may indicate an unusually well developed iliocostalis muscle system. Such an arrangement, with the ribs acting as lateral levers, would efficiently produce lateral flexure. The result would emphasize a reptilian, rather than a mammalian, mode of locomotion. It is certain that the imbrication of costal plates, whether of the galesaurid or advanced cynodont type, served to greatly strengthen the vertebral column. Functionally this may represent an early "experiment" in musculoskeletal adaptation to sustain a more characteristically mammalian posture with the trunk persistently held off the ground.

7) The cynodont shoulder girdle consists of a scapula, coracoid, procoracoid, clavicle and interclavicle. The coracoid has an elongate posterior process, as in monotremes, and is not so reduced as is commonly illustrated. The glenoid faced posterolaterally and slightly ventrally; the long axis of the scapular blade was inclined about 25° anteriorly.

8) Evolutionary modifications of the shoulder girdle during the reptilian-mammalian transition appear to have been related to changes in forelimb posture and con-

sequently in forelimb mechanics. In pelycosaurs, substantial compressive force on the thorax was generated by the posture of a laterally-directed, horizontally-held humerus. This force was accommodated by a large scapulocoracoid plate and robust clavicles. In cynodonts the humerus was held at an angle of about 45° to the longitudinal body axis; its distal end was somewhat depressed relative to the proximal end. As a consequence compressive force on the thorax was reduced, and so was the relative size of the scapulocoracoid plate and clavicles. The lateral bowing of the cynodont scapula probably oriented the serratus musculature in a manner which offset much of the residual compressive forces.

9) In pelycosaurs the screw-shaped glenoid provided a set trackway which predetermined humeral excursion during all phases of locomotion. Such a mechanism is perhaps indicative of a primitive state of neuromuscular coordination. Humeral excursion primarily involved anteroposterior movement in an essentially horizontal plane, plus rotation about the long axis of the humerus. In cynodonts no vestige of the primitive screw-shaped glenoid remained. Much of the propulsive thrust was transmitted to the scapula as in mammals. Anteroposterior movement of the humerus involved a significant amount of depression and elevation of the distal end, thus presaging the mammalian condition. It is likely that some longitudinal rotation, a primitive characteristic, was retained.

10) The cynodont forelimb is robust, a feature that results as much from the comparatively large size of the head as from the forelimb's "primitive" morphology. In normal stance, the radius crossed over the distal end of the ulna from lateral to medial side, as in the mammalian position of pronation.

11) There are eleven carpals in *Thrinaxodon*, the only cynodont for which a complete carpus is adequately known. The digital formula of *Thrinaxodon* is 2-3-4-4-3, with a disc-like, vestigial phalanx in digits III and IV; it is probable that later cynodonts had a mammalian count of 2-3-3-3-3. In *Diademodon*, at least, the forefoot is substantially larger than the hindfoot.

12) The cynodont pelvis shows a number of major modifications of the pelycosaurian pattern. The anterodorsal expansion of the iliac blade is unquestionably related to the growth and reorientation of the gluteal musculature which, as Romer (1922b) suggested, approximates a mammalian condition; moreover, the increase in iliac blade length allowed the sacrum to include five vertebrae and thereby form a stronger sacroiliac articulation. The pubis is considerably shorter than in pelycosaurs but otherwise retains a pelycosaurian pattern. There is no evidence that cynodonts possessed separate prepubic ("marsupial") bones. A large obturator foramen of mammalian proportions is developed. The acetabulum is better ossified than in pelycosaurs and approximates a mammalian morphology in its socket-like shape and slightly ventral orientation.

13) In larger cynodonts the femoral head is well ossified, bulbous and reflected mediodorsally. The tibial facets on the distal end of the femur are neither parallel to the femoral axis as in pelycosaurs nor arranged in pulley-like fashion across the distal

end as in mammals; instead they are planar and lie at angles of about 45° to the femoral axis. This condition appears to be intermediate but depending on the disposition of the overlying cartilage may have closely resembled the mammalian pattern which permits a large degree of flexion and extension.

14) Consideration of the articular relationships on the hindlimb shows cynodonts to be intermediate between pelycosaurs and generalized mammals with regard to femoral posture. In pelycosaurs the femoral axis makes about an 80° angle with the body in normal stance; the distal end of the femur is slightly elevated relative to the proximal end. In cynodonts the same angle is about 55° compared with 25° in generalized mammals; the distal end of the cynodont femur is held below the level of the acetabulum but not as far ventrally as in mammals.

15) The origin of the mammalian lesser trochanter is reviewed with reference to the theories of Romer (1924) and Parrington (1961). Romer held that the trochanter on the anteroventral aspect of pelycosaur and therapsid femora is not homologous with the mammalian lesser trochanter because non-homologous muscles attach to each. Parrington concluded that the cynodont anteroventral trochanter is homologous with the mammalian lesser trochanter, although the pelycosaur trochanter in the same position is not. Parrington believed with Romer that the reptilian internal trochanter migrated posteriorly in the mammalian lineage and was lost; it was purportedly replaced by the lesser trochanter which migrated ventrally to assume the position of the displaced internal trochanter. The evidence for trochanter migration is questionable. It is here proposed that: i) there has been only one anteroventral trochanter in synapsids on or close to the line of mammalian ancestry; ii) a slight shift in muscle insertion accounts for the fact that non-homologous muscles insert on this trochanter in living reptiles and mammals; iii) the mammalian pattern of muscle insertion is functionally related to the repositioning of the hindlimb.

16) The plantigrade cynodont pes possesses numerous features well advanced toward a mammalian pattern. The sustentaculum tali and tuber calcis are large. The astragalus was at least as much supported by the calcaneum as by its own plantar contact, presaging the mammalian condition in which the astragalus lies entirely upon the calcaneum. The two separate calcaneo-astragalar facets are aligned obliquely to the calcaneal axis, a condition intermediate between that of pelycosaurs, in which they are parallel, and that of mammals, in which they are nearly transverse. The wedge-shaped cuneiforms and cuboid of cynodonts are evidence of the development of a mammalian type of transverse arch. The cynodont foot was relatively narrow and possessed complex intermetacarpal articulations, as in mammals. The phalangeal formula, of advanced cynodonts at least, is 2-3-3-3-3. Comparison of the pes of *Bauria* with that of an advanced cynodont shows that the latter is more advanced toward a mammalian pedal morphology than the former.

17) The less complete ossification in the appendicular skeleton of smaller cynodont genera creates apparent differences in morphology when compared to the better ossified limb bones of larger genera. If allowances are made for this fact, then it is clear

that the postcranial skeleton of cynodonts is remarkably uniform in morphology. Only in rib design do cynodonts display the tendency toward rapid evolutionary change in the postcranial skeleton.

18) There is no osteological evidence as yet that cynodonts possessed a diaphragm as suggested by Brink (1954, 1955, 1956). Moreover, there is no evidence of bony epiphyses. It is certain that cynodonts did not possess bony epiphyses but the question of a diaphragm cannot be settled either way with known material.

19) In details of morphology and function, the cynodont postcranial skeleton should be regarded as neither "reptilian" nor "mammalian" but as transitional between the two classes. It is inappropriate to conceive of cynodonts as representing a prototherian level of organization, for in many ways the monotreme postcranial skeleton is highly specialized. If indeed a cynodont is the common ancestor of all living mammals, then it is appropriate to examine the monotreme skeleton for cynodont characteristics, not vice versa.

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The Morphology of the Syrinx in Passerine Birds

Peter L. Ames

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OF NATURAL HISTORY
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The Morphology of the Syrinx in Passerine Birds

PETER L. AMES
Encyclopaedia Britannica
425 North Michigan Avenue
Chicago, Illinois 60611

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THE MORPHOLOGY OF THE SYRINX IN PASSERINE BIRDS

PETER L. AMES

ABSTRACT

The syrinx, for more than a century an important organ in determining the subdivisions of the avian order Passeriformes (perching birds), was examined in 983 specimens, representing 65 of the 67 families recognized by most modern authorities. Particular emphasis was placed on the suborder Tyranni and especially on the family Tyrannidae (tyrant flycatchers).

The three general morphological categories established by Müller in 1847 form the basis for the major subdivisions now in use. Of Müller's divisions, two appear valid taxonomic units: the "Tracheophonae" (the modern superfamily Furnarioidea) and the "Polymyodae" (the suborder Passeres or oscines, often called songbirds). Müller's third category, the "Picarii," contains both simple and relatively complex syringeal types. Taxonomic decisions based on the simple type (in which intrinsic muscles and cartilaginous elaborations are lacking) should be made cautiously, since it apparently represents the ancestral "pico-passerine" syrinx. Certain results of this study suggest changes in the current classification of the Passeriformes.

1) The antbird-ovenbird complex, now usually considered a superfamily (Furnarioidea) in the suborder Tyranni, should be elevated to subordinal rank (Furnarii). This group is characterized by a highly specialized vocal apparatus that sets them apart from other passerines. There are, moreover, no other structural characters that ally this group to any other passerine group in particular.
    a) The Furnariidae (ovenbirds) are closest to the Dendrocolaptidae (woodcreepers), but may be separated from them by the absence (except in *Geositta*) of dorsal and ventral "horns" on the Processi vocales.
    b) The Formicariidae (antbirds) fall into two structural groups, based on several features of the syrinx, reinforced by external characters. These may be called "typical antbirds" (*Thamnophilus* and others) and "ground antbirds" (*Grallaria, Conopophaga* and others).
2) The Cotingidae (cotingas), as presently classified, include several syringeal types.
    a) *Attila, Casiornis, Rhytipterna* and *Laniocera* appear to be more closely related to the Tyrannidae, especially to *Myiarchus,* than to the more colorful cotingas, with which they are usually placed, but from which they differ in possessing oblique intrinsic muscles and internal cartilages. The becards (*Pachyramphus* and *Platypsaris*) also appear to belong with the Tyrannidae.
3) In the Tyrannidae (tyrant flycatchers) the syrinx is characterized by the presence of oblique intrinsic muscles and internal cartilages. There are several structural

groups, varying in homogeneity. In general, these groups support the classification of Hellmayr (1927).

   a) *Sayornis* appears to be closer to *Empidonax* and *Nuttallornis* than to the *Fluvicola* group.
   b) *Myiozetetes, Sirystes* and *Legatus* do not appear to belong in the middle of a linear series that includes *Muscivora, Tyrannus, Empidonomus, Myiodynastes, Megarhynchus, Pitangus* and *Tolmarchus.*
   c) The subfamily Platyrinchinae, characterized by broad, flat bills, seems to be an artificial assemblage, if the wide differences in syringeal structure among the three genera (out of the five) studied are considered.
   d) The genera *Terenotriccus, Pyrrhomyias, Myiobius* and *Onychorhynchus,* along with the manakin *Piprites,* form a group characterized by the absence of intrinsic muscles and (in most) by syringeal asymmetry.

4) The sharpbill (*Oxyruncus*) has the oblique intrinsic muscles and internal cartilages characteristic of the Tyrannidae, but the details of the syrinx are not of much help in determining to which group of tyrant flycatchers the sharpbill is closest.
5) Three small Old World families, the Pittidae, Philepittidae and Acanthisittidae, currently placed in the suborder Tyranni entirely on the basis of their syringeal structure, show no obvious relationship to any New World families. The syrinx of the Philepittidae is remarkably like that in the broadbills *Psarisomus* and *Serilophus,* with which *Philepitta* shares certain features of the sternum and pterylosis. The Philepittidae may well be more closely related to the Eurylaimidae than to the Tyranni or the Furnarii.
6) The scrub-birds (Atrichornithidae) are more like the lyrebirds (Menuridae) in syringeal structure than previously believed. Both have three pairs of intrinsic muscles, arranged in a pattern much like that found in songbirds (Passeres).
7) The suborder Passeres has been extensively studied. It is far less variable in syringeal structure than the Tyranni or Furnarii. The syrinx is complex but uniform throughout the suborder, suggesting that the group is narrowly monophyletic. The absence of the pessulus in the larks (Alaudidae) should not be considered primitive, for its absence is almost certainly secondary. The pessulus is present in most suboscines and in the nonpasserine orders Piciformes and Coraciiformes, and was probably present in the ancestor of the Passeres.

ZUSAMMENFASSUNG

Die Syrinx, seit mehr als einem Jahrhundert dazu benutzt, die Gattungen der Passeriformes (Sperlingsvögel) von einander abzugrenzen, wurde bei 983 Exemplaren untersucht, Material, das sich auf 65 der 67 von den meisten modernen Sachverständigen anerkannten Familien verteilt. Besondere Aufmerksamkeit wurde der Unterordnung der Tyranni zugewandt, hauptsächlich der Familie der Tyrannidae.

Die drei von Müller 1847 aufgestellten Kategorien bilden die Grundlage für die Hauptunterteilungen, die jetzt gebräuchlich sind. Von Müller's Gruppen scheinen zwei

wohlbegründete taxonome Einheiten zu sein: die "Tracheophonae" (die moderne Superfamilie der Furnarioidea) und die "Polymyodae" (die Unterordnung der Passeres oder Oscines, oft Singvögel genannt). Müller's dritte Einheit, die "Picarii", enthält sowohl einfache als auch relativ komplizierte Syrinx-Typen. Taxonomische Entscheidungen, die auf dem einfachen Typus (bei dem "intrinsische" Muskeln und knorpelige Bereicherungen fehlen) begründet sind, sollten mit Vorsicht gehandhabt werden, da dieser Typ anscheinend die ursprüngliche "pico-passerine" Syrinx darstellt. Bestimmte Ergebnisse dieser Untersuchung legen Änderungen in der gegenwärtigen Einteilung der Passeriformes nahe.

1) Der Ameisenvögel-Töpfervögel-Komplex, der zur Zeit gewöhnlich als eine Superfamilie (Furnarioidea) in der Unterordnung der Tyranni betrachtet wird, sollte in den Rang einer Unterordnung (Furnarii) erhoben werden. Diese Gruppe wird charakterisiert durch einen sehr spezialisierten Stimmapparat, der sie von den anderen Passerinen unterscheidet. Ausserdem gibt es keine anderen Strukturmerkmale, die diese Gruppe mit irgendeiner anderen Sperlingsvögel-Gruppe besonders verbindet.
    a) Die Furnariidae (Töpfervögel) stehen den Dendrocolaptidae (Baumsteiger) am nächsten, können aber von ihnen getrennt werden durch das Fehlen von dorsalen und ventralen "Hörnern" der Processi vocales (ausgenommen *Geositta*).
    b) Die Formicariidae (Ameisenvögel) zerfallen hinsichtlich mehrerer Merkmale ihrer Syrinx in zwei Gruppen, was äussere Kennzeichen bekräftigen. Sie können als "typische" Ameisenvögel (*Thamnophilus* und andere) und "Boden"-Ameisenvögel (*Grallaria, Conopophaga* und andere) bezeichnet werden.
2) Die Cotingidae (Kotingas) wie sie zur Zeit zusammengefasst werden, weisen mehrere Syrinx-Typen auf.
    a) *Attila, Casiornis, Rhytipterna* und *Laniocera* scheinen mit den Tyrannidae, besonders mit *Myiarchus,* näher verwandt zu sein als mit den farbigeren Formen, mit denen sie gewöhnlich zusammengestellt werden, von denen sie sich aber unterscheiden indem ihnen schräge, "intrinsische" Muskeln und innere Knorpel eigen sind. Die *Pachyramphus-* und *Platypsaris-*Arten scheinen auch zu den Tyrannen zu gehören.
3) Bei den Tyrannidae wird die Syrinx gekennzeichnet durch das Vorhandensein von schrägen, "intrinsischen" Muskeln und inneren Knorpeln. Es gibt mehrere Struktur-Gruppen, die in ihrer Gleichartigkeit variieren. Im allgemeinen bestätigen diese Gruppen die Einteilung von Hellmayr (1927).
    a) *Sayornis* scheint *Empidonax* und *Nuttallornis* näher zu stehen als der *Fluvicola*-Gruppe.
    b) *Myiozetetes, Sirystes* und *Legatus* scheinen nicht in die Mitte der gradlinigen Reihenfolge zu gehören, die *Muscivora, Tyrannus, Empidonomus, Myiodynastes, Megarhynchus, Pitangus* und *Tolmarchus* einschliesst.
    c) Die Unterfamilie Platyrinchinae, die durch breite, flache Schnäbel gekennzeichnet wird, scheint eine künstliche Gruppe zu sein, wenn man die grossen Unterschiede in der Struktur der Syrinx zwischen den drei (von fünf) Gattungen, die untereucht wurden, bedenkt.
    d) Die Gattungen *Terenotriccus, Pyrrhomyias, Myiobius* und *Onychorhynchus* zusammen mit der Pipride *Pipites*, bilden eine Gruppe, die durch das Fehlen

von "intrinsischen" Muskeln und (in den meisten Fällen) durch das Vorhandensein von Asymmetrie der Syrinx gekennzeichnet wird.

4) Der Flammenkopf (*Oxyruncus*) hat die schrägen, "intrinsischen" Muskeln und die inneren Knorpel, die die Tyrannidae kennzeichnen, indessen tragen die Einzelheiten des Syrinxbaues wenig dazu bei um zu bestimmen, welcher Gruppe der Tyrannen er am nächsten steht.
5) Drei kleine Familien der Alten Welt, die Pittidae, Philepittidae und Acanthisittidae, die zur Zeit lediglich auf Grund der Struktur ihrer Syrinx in der Unterordnung der Tyranni eingeordnet werden, zeigen zu keiner der neuweltlichen Familien eine offensichtliche Verwandtschaft. Die Syrinx der Philepittidae ist auffallend ähnlich derjenigen der Eurylaemiden *Psarisomus* und *Serilophus*, mit denen sie bestimmte Merkmale des Brustbeines und der Pterylose teilen. Die Philepittidae dürften wohl näher mit den Eurylaimidae verwandt sein als mit den Tyranni oder den Furnarii.
6) Die Atrichornithidae sind in der Struktur ihrer Syrinx den Leierschwänzen (Menuridae) ähnlicher, als man bisher geglaubt hat. Beide haben drei Paare "intrinsischer" Muskeln, die in einer Weise angeordnet sind, die derjenigen der Singvögel (Passeres) sehr ähnlich ist.
7) Die Unterordnung der Passeres wurde eingehend untersucht. Sie ist in der Struktur ihrer Syrinx weit weniger variabel als die Tyranni oder die Furnarii. Die Syrinx ist kompliziert, aber in der Unterordnung überall einheitlich, was nahelegt, dass die Gruppe streng monophyletisch ist. Das Fehlen des pessulus bei den Lerchen (Alaudidae) sollte nicht als primitiv angesehen werden, da dieser Mangel sekundär sein dürfte. Der pessulus ist bei den meisten Suboscines und bei den nicht-passeriformen Ordnungen der Piciformes und Coraciiformes vorhanden und war wahrscheinlich auch bei den Vorfahren der Passeres ausgebildet.

RESUMEN

La siringe, utilizada por más de un siglo como órgano importante para determinar las subdivisiones del orden Passeriformes (pájaros), fué examinada en 983 ejemplares, representando 65 de las 67 familias reconocidas por la mayoría de las autoridades modernas. Se puso atención especial en el suborden Tyranni y sobretodo en la familia Tyrannidae (atrapamoscas tiranas).

Las tres categorías generales morfológicas establecidas por Müller en 1847 forman la base de las subdivisiones más importantes ahora en uso. De las divisiones de Müller, dos de ellas parecen ser unidades taxonómicas válidas: las "Tracheophonae" (la superfamilia moderna Furnarioidea) y las "Polymyodae" (el suborden Passeres u oscines, frecuentemente llamados pájaros canoros). En la tercera categoría de Müller, los "Picarii", se encuentran siringes de forma sencilla así como otras de forma compleja. Decisiones taxonómicas basadas en el tipo sencillo (en el cual los músculos intrínsecos y las elaboraciones cartiloginosas no existen) deben ser hechas cautamente, porque aparentemente este tipo representa la siringe "pico-paserino" ancestral. Algunos resultados de este estudio sugieren cambios en la clasificación actual de los Passeriformes.

1) El grupo hormiguero-hornero, considerado usualmente hoy en día como una superfamilia (Furnarioidea) en el suborden Tyranni, debe ser elevado a la categoría de suborden (Furnarii). Este grupo se caracteriza por poseer un aparato vocal altamente especializado que lo distingue de los otros grupos paserinos. Además, no tiene ninguna otra característica estructural que lo una con ningún otro grupo paserino en particular.
   a) Las Furnariidae (horneros) tienen sus nexos mas cercanos con las Dendrocolaptidae (trepadores). Se distinguen de éstas por la ausencia (excepto en *Geositta*) de eminencias corniformes dorsales y ventrales en los Processi vocales.
   b) Las Formicariidae (hormigueros) pueden divisarse in dos grupos estructurales basados en algunas características de la siringe que muestran cierto paralelismo con algunos caracteres externos. Estos pueden llamarse "hormigueros típicos" (*Thamnophilus* y otros) y "hormigueros terricolas" (*Grallaria, Conopophaga* y otros).
2) Las Cotingidae (cotingas), como son clasificadas actualmente, contienen varios tipos de siringe.
   a) *Attila, Casiornis, Rhytipterna* y *Laniocera* parecen estar mas relacionados con las Tyrannidae, especialmente con *Myiarchus,* que con las coloridas cotingas, entre las cuales están usualmente incluídos. Se diferencian de éstas por poseer músculos oblicuos y cartílagos internos. Los picos gruesos (*Pachyramphus* y *Platypsaris*) también parecen pertenecer a las Tyrannidae.
3) Entre las Tyrannidae (atrapamoscas tiranas), la siringe se caracteriza por la presencia de músculos intrínsecos oblicuos y cartílagos internos. Hay varios grupos estructurales, variando en homogeneidad. En general estos grupos respaldan la clasificación de Hellmayr (1927).
   a) *Sayornis* se acerca más a *Empidonax* y *Nuttallornis* que al grupo *Fluvicola.*
   b) *Myiozetetes, Sirystes* y *Legatus* parecen estar mal colocados en su posición actual, en medio de una serie linear que incluye *Muscivora, Tyrannus, Empidonomus, Myiodynastes, Megarhynchus, Pitangus* y *Tolmarchus.*
   c) La subfamilia Platyrinchinae, caracterizada por picos anchos y aplastados, parece ser una agrupación artificial, considerando las amplias diferencias de estructura en la siringe de los tres géneros (entre cinque) estudiados.
   d) Los géneros *Terenotriccus, Pyrrhomyias, Myiobius* y *Onychorhynchus,* junto con el saltarín *Piprites,* forman un grupo caracterizado por la ausencia de músculos intrínsecos y (en la mayoría) por asimetría de la siringe.
4) El picoagudo (*Oxyruncus*) posee músculos oblicuos intrínsecos y cartílagos internos característicos de los Tyrannidae, pero los detalles de la siringe no son de mucha ayuda para determinar los nexos más cercanos que tiene el picoagudo dentro del grupo de las atrapamoscas tiranas.
5) Tres familias pequeñas del Antiguo Mundo, las Pittidae, las Philepittidae y las Acanthisittidae, son corrientemente colocadas en el suborden Tyranni a base unicamente de la estructura de la siringe, pero no muestran ninguna relación obvia con ninguna de las familias del Nuevo Mundo. La siringe de las Philepittidae es notablemente parecida a la de los picoanchos *Psarisomus* y *Serilophus,* con los cuales *Philepitta* comparte ciertas características del esternón y del pterylosis. Es muy posible que las Philepittidae estén relativamente más cerca de las Eurylaimidae que de los Tyranni o los Furnarii.

6) Los pájaros-rastrojeros (Atrichornithidae) son más parecidos a los pájaros cola de lira (Menuridae) en la estructura de la siringe de lo que antes se creía. Ambos tienen tres pares de músculos intrínsecos, colocados de una manera muy parecida a la de los pájaros canoros (Passeres).
7) El suborden Passeres ha sido estudiado extensamente. Es mucho menos variable en la estructura de la siringe que los Tyranni o los Furnarii. La siringe es compleja pero uniforme en todo el suborden, sugiriendo que el grupo pueda ser estrechamente monofilético. La ausencia del pessulus en las alondras (Alaudidae) no debe considerarse como carácter primitivo, puesto que su falta es muy probablemente una condición secundaria. El pessulus está presente en casi todos los suboscines y también en los órdenes no-paserinos Piciformes y Coraciiformes; muy probablemente estaba presente en la forma ancestral de los Passeres.

РЕЗЮМЕ

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Нижняя гортань (сиринкс) уже свыше столетия считается важным органом при установлении подразделений птичьего отряда Passeriformes (воробьиных); она сейчас изучена у 983 экземпляров, представляющих собой 65 семейств из тех 67, которые признаны большинством современных авторитетов. Особое значение придавалось подотряду Tyranni и, главным образом, семейству Tyrannidae (тираннов).

Три общие морфологические категории, установленные Мюллером в 1847 г., являются основанием для главных подразделений, которыми пользуются теперь. Из трёх разрядов Мюллера, два представляют, повидимому, обоснованные таксономические разряды: "Tracheophonae" (современное надсемейство Furnarioidae) и "Polymyodae" (подотряд Passeres или певчих воробьиных, называемый часто певчими птицами). Третий разряд Мюллера "Picarii" содержит как простые, так и сравнительно сложные виды нижних гортаней птиц. Таксономические решения, основанные на свойствах нижней гортани простого вида (у которой отсутствуют внутренние мышцы и хрящевые утончения) следует делать осторожно, так как простой тип нижней гортани представляет, повидимому, наследственную "дятло-воробьиную" нижнюю гортань. Некоторые результаты данного исследования наводят на мысль о внесении изменений в современную классификацию Passeriformes.

1) Совокупность птиц муравьеловок и печников, которая в настоящее время рассматривается, чаще всего, как надсемейство (Furnarioidea) в подотряде Tyranni следует возвысить в ранг подотряда (Furnarii). Эта группа отличается крайней специализацией голосового аппарата, что отделяет её от других воробьиных. Кроме того отсутствуют какие бы то ни было структурные особенности, которые связывали бы эту группу, в частности, с другими воробьиными.
   a) Furnariidae (печники) состоят в ближайшем родстве с Dendrocolaptidae (древолазве Южной Америки), но могут быть отделены от них ввиду отсутствия (за исключением у Geositta) спинных и брюшных "рогов" на Processi vocales. Formicariidae (муравьеловки) делятся на две группы строения, что обусловлено несколькими особенностями нижней гортани, которые подкреплены внешними деталями. Эти группы можно назвать: "типичными муравьеловками" (Thamnophilus и др.) и "наземными муравьеловками" (Grallaria, Conopophaga и др.).

2) Cotingidae (котинги), согласно классификации существующей в настоящее время, охватывают несколько типов нижних гортаней.
   a) Attila, Casiornis, Rhytipterna и Laniocera состоят, вероятно, в более близком родстве с Tyrannidae и в особенности с Myiarchus, чем с более красочными котингами, к которым их обыкновенно относят, но от которых они отличаются тем, что имеют наклонные внутренние мышцы, а также и внутренние хрящи.
   b) Бекарды (Pachyrampus и Platypsaris) тоже относятся, повидимому, к Tyrannidae.

3) У Tyrannidae (тиранков) нижняя гортань характеризуется наличием наклонных внутренних мышц и внутренних хрящей. Существует несколько структурных групп, степень однородности которых не одинакова. Вообще же эти группы подтверждают классификацию Hellmayr (1927).
   a) Sayornis находятся, вероятно, в более близком родстве с Empidonax и Nuttallornis, чем с группой Fluvicola.
   b) Myiozetetes, Sirystes и Legatus, очевидно, не следует помещать в середине линейной серии, включающей Muscivora, Tyrannus, Empidonomus, Myiodynastes, Megarhynchus, Pitangus и Tolmarchus.
   c) Подсемейство Platyrinchinae, которое характеризуется широкими и плоскими клювами, кажется искусственный конгиомератом, если принять во внимание значительные различия в устройстве нижней гортани и трёх видов (из пяти), которые были изучены.
   d) Виды Terenotriccus, Pyrrnomyias, Myiobius и Onychorhynchus, наряду с манакинами Piprites, образуют группу, которая отличается отсутствием внутренних мышц и (у большинства) асимметрией нижней гортани.

4) Остроклюв (Oxyruncus) имеет и наклонные внутренние мышцы, и внутренние хрящи, характерные для Tyrannidae, однако, детали нижней гортани мало помогают диявияскение толо, с какой группой тираннов остроклюв состоит в ближайшем родстве.

5) Три небольших семейства Старого Света, Pittidae, Philepittidae и Acanthisittidae, относимые в настоящее время к подотряду Tyranni, всецело на основании строения их нижних гортаней, не имеют явной связи с каким бы то ни было семейством Нового Света. Нижняя гортань Philepittidae замечательно похожа на нижнюю гортань ширококлювов Psarisomus и Serilophus, с которыми у Philepitta имеется ряд общих черт в устройстве грудины и птерилия. Вполне возможно, что Philepittidae находятся в более близком родстве с Eurylaimidae, чем с Tyranni или с Furnarii.
6) Строение нижней гортани у атрихий (Atrichornithidae) и у лировостов (Menuridae) более однородно, чем предполагалось раньше. У обеих гортаней три пары внутренних мышц, расположенных по типу, который напоминает во многих отношениях устройство нижней гортани у певчих птиц (Passeres).
7) Подотряд Passeres подробно изучен. Различия в устройстве нижней гортани у этих птиц гораздо менее значительны, чем у Tyranni или у Furnarii. Нижняя гортань сложная, но однородная у всего подотряда, что указывает на строгую монофилию группы. Отсутствие у жаворонков (Alaudidae) поперечной болтоподобной кости или хряща при разветлении трахеи на бронхи (pessulus — болт) не следует считать признаком примитивности, так как почти наверняка отсутствие её явствовать вторичный признанный. Болтоподобное устройство существует у большинства представителей подотряда певчих птиц, а также и у неворобьиных отрядов Piciformes и Coraciiformes, по всей вероятности, оно имелось и у предков Passeres.

HISTORY OF SYRINGEAL MORPHOLOGY

The syrinx was first described by Herissant (1753) who recognized it as the source of voice in the domestic duck. Vicq D'Azyr (1779) described the passerine syrinx for the first time and believed that the syrinx of songbirds represented the simplest form. Cuvier (1802) examined the syrinx of the European Starling (*Sturnus vulgaris*), concluding that its morphology was far more complex than suggested by Vicq D'Azyr. Savart (1826) described the syrinx of songbirds in more detail, naming the muscles on the basis of their action. He noted a membrane extending anteriorly from the pessulus and called it the "*Membrana semilunaris.*" Yarrel (1833) examined the syrinx of the Raven (*Corvus corax*) but added little to previous descriptions.

Nitzsch (1829) described the syringes of many European passerines and nonpasserines. He was the first to apply syringeal morphology to the classification of birds. In this he was not very successful, but he did show that the "singing birds" have a strongly muscled syrinx.

The earliest descriptions of the syrinx in New World passerines, including many of the Tyranni, were those of MacGillivray (1838). He described the vocal organs of *Tyrannus, Myiarchus, Contopus,* and *Empidonax* and noted that the pessulus is lacking "in *Tyrannus* as in all the New World Muscicapidae." He also described the syringeal structure in thirty-nine genera of oscines, belonging to many families. MacGillivray's examination was frequently of a superficial nature, as indicated by his belief that the principal differences in syringeal structure were in the degree of development. Blyth (1838) examined the vocal organ in a few cotingas, manakins, and tyrant flycatchers and concluded, after a rather superficial examination, that it was as complex as that of European passerines.

Eyton (1841-1844) produced the first description of the "tracheal" syrinx in *Upucerthia, Furnarius, Cinclodes,* and *Synallaxis.* In other papers he described the Lyrebird *Menura* (1841) and *Gymnorhina* (1842). Like many of his predecessors, Eyton apparently suffered from inadequate magnifying equipment, for in *Menura* he overlooked a pair of muscles later described by Garrod (1876). Eyton was primarily interested in the Mm. sternotracheales and in a great number of cases he "described" the syrinx entirely in terms of these muscles.

Müller (1847, 1878) examined the syringes of more genera of birds than anyone before him. He separated the "American Muscicapidae" (Tyrannidae) from the Old World (true) Muscicapidae on the basis of the degree of development of their syringeal muscles. He was the first to provide a systematic arrangement of the Passeriformes based on syringeal morphology, and to relate the form of the syrinx to other anatomical characters, particularly the scutellation of the tarsus. Müller's work has been the foundation for all subsequent classifications in which the syrinx has been used as a taxonomic character.

Herre (1859) and Owen (1866) described the syringeal structure of many European passerines, but added little new information. Owen's nomenclature for the oscine syringeal muscles has been used by most subsequent writers in English.

Garrod (1876, 1877a) described the syrinx of many non-oscine genera, including *Menura*, *Atrichornis*, *Pitta*, and several other Tyrannoidea. He coined the terms "mesomyodian" and "acromyodian," referring to the position of the insertion of the intrinsic muscles. Forbes, a pupil of Garrod, described the syrinx in the broadbills *Eurylaimus* and *Cymbirhynchus* (1880a), in *Acanthisitta* and *Xenicus* (1882), in *Conopophaga* (1881), and in *Philepitta* (1880b). The study of *Acanthisitta* was repeated by Pycraft (1905a).

Wunderlich (1886) described the syrinx in a large number of European birds, including a few passerines. His most significant contribution was in the embryology of the syrinx, which he studied in the domestic duck and in the House Sparrow (*Passer domesticus*). Furbringer (1888) summarized the work of previous authors and coined the word "diacromyodian" for the condition in which the muscles insert at both ends of a single element.

Gadow and Selenka (1893) collated the findings of previous authors and provided an original description of the syrinx in the European Crow (*Corvus corone*). Because their description and nomenclature were to be so extensively used by later investigators, it is particularly unfortunate that their illustrations of *Corvus* contain four errors in labeling muscles.

Haecker (1900) was primarily interested in the means and function of sound production. With histological sections he demonstrated differences in muscles and in cartilages between sexes and age groups in several species of European passerines.

Setterwall (1901) studied the syringeal structure of a large number of Palearctic songbirds. He concerned himself with some of the less studied aspects of the syrinx, such as individual variation. He looked carefully at the interior of the syrinx and was particularly interested in the small cartilaginous elements. Setterwall's theories on the function of the syrinx were to have considerable effect on the studies of Rüppell (1933) and Greenewalt (1968).

By the turn of the century it was a common practice to include a description of the syrinx in the systematic morphology of a species. More often than not, such inclusions were exeremely brief, such as Pycraft's (1905b) mention that the syrinx of the Wren Thrush (*Zeledonia*) is "typically oscine." It was the beginning of an era in which many passerines were to be classified largely on the basis of syringeal structure. Bates (1914) used the morphology of the syrinx of *Smithornis stongei* to remove that genus from the oscine family Muscicapidae and ten years later Lowe (1924) compared the syrinx of *S. rufolateralis* with that of *Eurylaimus*, in placing *Smithornis* in the Eurylaimidae. The rare Grauer's Broadbill (*Pseudocalyptomena*) was placed by Lowe (1931) in the Eurylaimidae on the basis of the syrinx and some other characters.

Köditz (1925) studied the syringeal morphology in a number of species of the families Pycnonotidae, Meliphagidae, Nectariniidae, Irenidae, Zosteropidae, Pittidae, and Eurylaimidae. He pointed out that apparent variations in the number of oscine syringeal muscles are more often due to differences in nomenclatorial concepts than to actual differences in syringeal structure.

Maynard (1928) studied the syrinx in a number of passerines and non-passerines, taking careful measurements of many parts of the respiratory system. Unfortunately, his book is illustrated with woodcuts which give only a vague impression of syringeal structure. His apparent lack of good magnifying equipment is indicated by the many inaccuracies in the descriptions.

The twentieth century has seen a number of passerine genera moved from one suborder to another, partly or wholly on the basis of syringeal morphology. *Melampitta* (Mayr, 1931), *Lawrencia* (Wetmore and Swales, 1931), and *Ramphocaenus* (Wetmore, 1943) were shown to be oscines. *Psilorhamphus*, thought to be a close relative of *Ramphocaenus*, was proven by Plótnick (1958) to belong in the furnarioid family Rhinocryptidae. Amadon (1951) showed through syringeal morphology that the Madagascar genus *Neodrepanis* is not oscine, but closely related to the peculiar Asities (Philepittidae).

The systematic positions of some passerines have been confirmed by syringeal morphology. The syrinx of the extinct Mascarene starling *Fregilupus* was described by Miller (1941) and in more detail by Berger (1957) who compared it with that of the Vanga Shrike *Artamella* and with the European Starling *Sturnus*. After comparing the syrinx of *Gymnorhina* with that of *Corvus*, Mayr (1931) affirmed that the Cracticidae are more closely related to the Corvidae than to the Laniidae. Mayr and Amadon (1951) examined the syrinx of the African River Martin *Pseudochelidon* and concluded that it merited subfamily separation from the other swallows.

In a lengthy paper devoted largely to the mechanics of sound production in non-passerines, Rüppell (1933) described the syrinx of the woodhewer *Lepidocolaptes*, naming the intrinsic muscles for the first time. Clark (1913) compared the syrinx of the Sharpbill *Oxyruncus* with that of the tyrannid *Sayornis*, concluding that the Sharpbill is a modified tyrannid. Kuchler (1936) used the morphology of the syrinx in the Plantcutter *Phytotoma* to relate that genus to the Cotingidae. Lowe (1942) used syringeal morphology to indicate evolutionary trends in some Pipridae.

One of the most significant studies of the passerine syrinx in recent years is that of Miskimen (1951), in which the vocal organs of twenty-nine oscine species and two tyrannids were described. Her statements on the range of variation in number of syringeal muscles among North American songbirds differed greatly from the accounts of Wunderlich, Haecker, Setterwall, and Köditz, all of whom studied Old World species. Miskimen's findings indicated that the total number of muscles varies from four to seven pairs and these figures have been linked to Setterwall's upper limit of nine pairs to suggest greater variability than was previously believed present. Miskimen performed *in vitro* experiments on the syrinx, repeating some of Rüppell's (1933) experiments. She was able to confirm that sound is produced on the expirant cycle of respiration and to show that the *membrana semilunaris* plays only a minor role in sound production.

In a more recent paper (1963) Miskimen described the syrinx in six genera of the Tyrannidae. She provided the most thorough description of the tyrannid syrinx to date and was the first to show clearly the oblique character of the ventral intrinsic muscles.

Greenewalt (1968) analysed the vocalizations of a wide spectrum of non-passerine and passerine birds. In addition to a detailed discussion of the acoustics of bird song, he set forth an hypothesis for the mechanism of sound production and modulation. Stein (1968) also analysed a number of bird vocalizations and proposed a theory of the operation of the syrinx, differing from that of Greenewalt on several points.

Chamberlain et al. (1968) studied the syrinx of the North American Crow (*Corvus brachyrhynchos*), with particular regard to the action of various muscles and their possible effect on the syringeal membranes.

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METHODS AND MATERIALS

METHODS OF DISSECTION AND PREPARATION.

The syrinx in passerine birds lies immediately anterior to the heart, surrounded by the interclavicular air sac. Descending the right side of the neck, the trachea enters the air sac at the base of the neck and shortly divides into the bronchi. The esophagus, which lies dorsal to the trachea for most of its length, passes between the bronchi near the tracheobronchial bifurcation. A small fibrous sheet, the bronchidesmus, joins the inner walls of the bronchi to the ventral surface of the esophagus. A tough silvery sheet, which Setterwall (1901) called the "syringeal aponeurosis," forms the anterior and dorsal walls of the air sac and is firmly attached to the trachea where the latter penetrates the air sac. The syrinx, located at the tracheobronchial junction, is too deep in the body cavity for study *in situ*. The use of formalin-preserved specimens facilitates the study of the minute syringeal muscles, which become firmer and easier to work with. Moreover, the majority of passerine birds are available only in anatomical "spirit" collections.

Many anatomists have found it convenient to remove the entire trachea, as well as the larynx and the tongue, for the study of the syrinx alone. In doing so they destroy most of the hyoid apparatus, which is itself of anatomical interest. I prefer a system of dissection that insures that the syrinx will be removed undamaged, while minimizing the damage to neighboring systems. Only the lower trachea, syrinx, bronchi, and a small section of esophagus are removed.

Once the interclavicular air sac has been opened and a visual inspection made to determine that the syrinx has not been destroyed by shot, which it occasionally is, a sagittal cut is made in the sternum and pectoral muscles a few millimeters to the right of the keel. In large birds (over 150 gm.) the sternal cut is omitted, unless the specimen is easily replaced. Next the trachea and esophagus are severed at the middle of the neck. A small scissors is used to cut the Mm. sternotracheales midway between origin and insertion. Failure to perform this cut usually results in the muscles being torn from the syrinx, where the attachment is often weak. The major blood vessels are now cut where they lie ventral to the bronchi (in large birds this cut can sometimes be omitted). A careful transverse cut across the posterior ends of the bronchi and esophagus frees the section of the respiratory and digestive tracts to be removed. With thin blunt forceps one can now lift the esophagus from the tissues dorsal to it and draw it anteriad, cutting the restraining connective tissue with a scalpel or fine scissors. By pulling only on the esophagus one draws the syrinx with it, minimizing the likelihood of damage to the syrinx.

In many large birds the size of the interclavicular air sac is sufficient to permit the removal of the syrinx with dental instruments, without cutting the sternum. Particularly necessary in this type of removal is a small scalpel, the blade of which lies in a plane at right angles to the handle. Considerably more time and care is needed, but the only significant damage to other organ systems is to the arteries of the region surrounding the syrinx.

After removal from the bird the syrinx is placed in a small dissecting dish for examination under binocular magnification of 20-60 ×. Usually some "clean-up" is necessary, removing preserved blood and body fluids, and peeling off the fine membranes which cover and obscure the muscles and cartilages. For gentle removal of unwanted surface material a fine artist's brush (00000 or smaller) is useful, aided by a jeweler's forceps. For further dissection I employ a variety of small scalpels and probes, ground from dental instruments.

For long-term storage, syringeal specimens are kept in an aqueous solution of 65 per cent ethanol and 10 per cent glycerine.

NOMENCLATURE.

Cartilaginous Elements.

In all passerines the middle of the trachea lies on the right side of the neck, twisted and laterally displaced relative to its ends. The dorsoventral orientation of the ends of the trachea corresponds to that of the bird, but in the middle section the "dorsal" side (determined by the position of the lateral muscles and nerves) lies against the side of the neck. The terms "ventral," "dorsal," "medial," and "lateral" are used here with respect to an idealized straight trachea, ignoring torsion and bending.

Previous authors, from Müller to Miskimen, have numbered the cartilaginous elements in two series, "tracheal" and "bronchial," numbering away from the point where the series meet. This point is the theoretical "tracheo-bronchial" junction. Traditionally those elements which are full circles are "tracheal rings"; those composed of paired semicircles or of two separate coplanar circles are "bronchial" semirings or rings. On this basis two individuals of the same species may appear to differ widely merely because fusion of elements has produced different starting points for the series. In the examination of the syringes of 784 species of 531 genera, I have found it impossible to name the supporting elements in the historical tracheal-bronchial sense. The elements do fall into two series, which I designate "A" and "B", based on the following criteria (see Pl. 1, fig. 2):

1) Cross section.
    Type A: flat and ribbon-like
    Type B: round or D-shaped
2) Consistency.
    Type A: transparent and stiff, often brittle
    Type B: whitish and opaque; spongy and flexible
3) Direction of concavity, other than toward axis of tube.
    Type A: directed posteriad
    Type B: directed anteriad

The A-series is always the more anterior of the two and, with no known exceptions, each series is continuous. Each series is numbered away from the point where the series meet.

The borderline between cartilage and bone in the passerine syrinx is not a sharp one. Very little true histological work was done in this study and the degree of ossification has not been quantitatively determined. Miskimen (1963) stated that, unlike the bony tracheal elements of the oscines, those of the Tyrannidae are cartilage. Some of the syringes of cotingas received from William Beebe, however, had been previously stained with alizarin using the method of Hollister (1934), which indicated the presence of calcium. The application of Von Kossa's Stain to sections of an adult phoebe syrinx (*Sayornis*) also indicated calcification of the tracheal elements, although less than in the Beebe specimens. Because the amount of calcification is much less than in the axial skeleton and because further histological work is needed to clarify the question, I will refer to all of the supporting elements of the syrinx as "cartilaginous."

The terms "ring" and "semiring," used by most authors to describe, respectively, the closed circular and the open semicircular elements, are inadequate to describe the variety of supporting cartilages in the passerine syrinx. The following adjectives are defined in the context of this paper (Pl. 1, fig. 1.):

1) Complete. The element forms a closed circle or ellipse.
2) Incomplete dorsally (or ventrally). The element forms a complete circle or ellipse except for a single opening near the dorsal (or ventral) midline.
3) Divided. The element consists of two halves, separated by openings near the dorsal and ventral midlines. The halves are mirror images, lie at approximately corresponding points relative to the tracheal axis, and are arcs of circles.
4) Double. The element consists of paired components, each of which is a closed loop. The loop need not be circular; the commonest type is D-shaped with the flat side directed medially. The halves may be 1) connected, i.e. fused more or less firmly in the region of contact, or 2) discrete, i.e. if in contact, able to move freely relative to each other.

When reference is made to one half of a divided or a double element the smaller part is termed a component, the word "element" being reserved for the entire structure. Reference to the right or left half of an element is indicated by an appropriate "R" or "L" added to the number of the element, viz: A-2R.

Unpaired components do occur, appearing as extra halves added to an otherwise symmetrical system. Such components are numbered with an "a" added to the number of the next lower element, and R or L to indicate the side. A-4aL is an unpaired component lying between A-4 and A-5 on the left side.

The pessulus is a bony or cartilaginous rod or narrow plate lying in the midsagittal plane of the trachea at the junction of the internal tympaniform membranes. Usually it is fused to other elements at its dorsal or ventral end, frequently at both. It may bear a small midsagittal membrane directed anteriorly, the *Membrana semilunaris*.

The drum is a cylinder composed of two or more complete A-elements fused along their entire lengths. Frequently the fusion is so complete that no seams remain to indicate how many elements comprise the drum. Miskimen (1963) used this term to designate the most posterior complete element or group of elements, in case of fusion. Functionally, a drum of fused elements provides a rigid support against compression of the trachea by muscles, so the term is inappropriate for a single unmodified element.

A *labium* is a cartilaginous pad or bar projecting into the lumen of the bronchus from the lateral ("*externum*") or medial ("*internum*") side. The *labia externa* are attached to the inner side of an A- or B-element; the *labia interna* are attached to the pessulus or are histologically continuous with it. Since my study did not usually involve opening the trachea or bronchi, the characteristics of the labia were seldom noted. What I have called the "cartilaginous plug" in the tyrannid syrinx may, in fact, be the result of extension and coalescence of the internal labia.

MEMBRANES.

Although the entire inner surface of the respiratory tract is a continuous epithelium, and another membranous sheet covers muscles and cartilaginous elements, in discussions of gross morphology the word "membrane" has traditionally been applied to a region between cartilaginous elements. In this sense, rather than a strictly histological one, the word is used here. Syringeal membranes vary in thickness and flexibility, sometimes blending imperceptibly into sheets of cartilage. Each discrete area of membrane is labeled by the elements surrounding it, the membrane between A-1 and B-1 being the "A-1/B-1 membrane."

Internal tympaniform membranes. This pair of membranes comprises most of the internal surface of the bronchi. They are supported at their edges by the ends of the divided A and B elements.

External tympaniform membranes. This name has usually been applied to the largest of the membranous areas on the lateral sides of the syrinx. The word "tympaniform" is inappropriate in most cases and the size of the membranes in preserved specimens is greatly influenced by the position of the syrinx in fixing. The term is not used in this paper.

MUSCLES.

The following muscles are extrinsic; they originate away from the syrinx and insert on it. Both are paired muscles. The terms "extrinsic" and "intrinsic" are used here with reference to the syrinx, not to the entire trachea, as is sometimes the case. An intrinsic tracheal muscle is an extrinsic syringeal one if it originates on a non-syringeal part of the trachea.

M. tracheolateralis. This thin, usually narrow muscle originates on the lateral surface of the cricoid cartilage of the larynx. It extends down the lateral surface of the trachea to insert on the ventral and/or lateral surfaces of one or more elements in the syringeal region.

M. sternotrachealis. This muscle originates on the internal surface of the coracoid or the costal process of the sternum, or on the internal surface of one or more ribs. Rarely, it originates on the inner surface of the intercostal muscles. It inserts on the lateral and/or ventral surface of the trachea, or on the tissues surrounding the trachea. Sometimes M. sternotrachealis is wholly or partly continuous with some of the fibers of M. tracheolateralis. Plótnick (1958) renamed this muscle M. costotrachealis in certain of the Furnarioidea, on the basis of its costal origin. While the new name is accurately descriptive, the basic position of the muscle is the same in the Furnarioidea as in virtually all other birds and the addition of the new name serves no useful purpose.

SOURCE OF SPECIMENS.

Most of the 983 specimens dissected in the course of this study were obtained from the alcohol collections of the Peabody Museum of Natural History (YPM), the United States National Museum (USNM), and the American Museum of Natural History (AMNH). The source of each specimen in the suborders Eurylaimi, Tyranni, and Menurae is given with the data in Appendix A. The details of the syringeal morphology of most of the oscines will be discussed in a series of future papers; only the names of the oscine species are given in Appendix B.

SYSTEMATICS USED IN THE MORPHOLOGICAL SECTION.

In the morphological sections that follow, the specimens are presented in taxonomic order, based on the prevailing classification of the present time. The arrangement of suborders, superfamilies, and families is that of Wetmore (1960). Below the family level there is no taxonomic revision covering the whole order Passeriformes. The most recent classification of the Eurylaimi, and the one followed here, is that of Peters (1951). For the New World Tyranni I have followed Hellmayr (1925-1929), except for the few cases in which a genus or species has been shown to have been placed by Hellmayr in the wrong superfamily or family. I have departed from Hellmayr's classification in including *Rupicola* in the Cotingidae. The nomenclature for the two species of the Menurae treated was drawn from Cayley (1931). For the Passeres I have employed the classification in available volumes of the *Check-list of Birds of the World* (Mayr and Greenway, 1960, 1962; Mayr and Paynter, 1964) and have filled the gaps from recent family revisions and regional works. (See references cited in the appropriate sections of Appendix B.)

The reader will find several instances in which generic names or allocations of species to genera and families are not what he would consider "prevailing classification." Such instances are frequent in Hellmayr's treatment of the Tyranni, which was followed closely on the grounds that the reader may always return to Hellmayr's work to clarify individual problems. In citing anatomical studies by previous authors, principally those of Müller (1847, 1878) and Garrod (1876, 1877a, b) I have employed the modern generic and specific names.

SYRINGEAL MORPHOLOGY

SUBORDER EURYLAIMI.

FAMILY EURYLAIMIDAE. BROADBILLS.

Specimens Examined.

Of the 14 species in eight genera, I have examined the following seven species in six genera:

Smithornis capensis (A. Smith)
Smithornis rufolateralis G. R. Gray
Cymbirhynchus macrorhynchus (Gmelin)
Eurylaimus javanicus Horsfield
Serilophus lunatus (Gould)
Psarisomus dalhousei (Jameson)
Calyptomena whiteheadi Sharpe

I know of only the following descriptions by previous authors:

Cymbirhynchus macrorhynchus (Gmelin) — Forbes (1880a)
Eurylaimus ochromalus Raffles — Forbes (1880a)
Pseudocalyptomena graueri Rothschild — Lowe (1931)
Smithornis sharpei Boyd Alexander — Bates (1914)
Smithornis sharpei Boyd Alexander — Lowe (1924)
Smithornis capensis (A. Smith) — Verheyen (1953, p. 184)
Smithornis rufolateralis G.R. Gray — Lowe (1924)
Corydon sumatranus (Raffles) — Müller (1847, p. 32; 1878, p. 27)

Müller's "description" of the syrinx of *Corydon* is merely a note on the lack of musculature.

Cartilaginous Elements.

In all species of *Smithornis* the cartilages are closely similar. A-1 and A-2 are divided, A-2 being oriented at an angle of about 45° to the sagittal plane of the trachea. A-3 and other A-elements are complete and all the B-elements are divided. There is no pessulus. My specimens agree closely with those of Lowe and, except for one detail, those of Verheyen. The latter was the only author to describe a drum in a broadbill. He does not state which elements are involved, but from his illustration and his statement that the drum has strengthening rings of "bronchial origin," it appears that the drum occupies the region of A-1 through A-3. In my specimens the A-1/A-2 and A-2/A-3 membranes are thick and leathery, but quite flexible. Verheyen's statement that the drum is continuous dorsally with the "bronchio-pulmonary" membranes leads me to believe that the "drum" was an artifact of preparation.

Eurylaimus and *Cymbirhynchus* are like *Smithornis*, with the following differences. A-1, described by Forbes as a "false ring," is shorter than B-1 and A-2 and floats in the membrane bounded by them. B-1 and A-2 are held together at their dorsal and ventral ends by fibrous connective tissue. The ventral half of A-1 is very narrow, about one quarter the width of the dorsal end, where it is as wide as the other A-elements. The pessulus is fused to A-3 at its dorsal and ventral ends. In the specimen of *Cymbirhynchus* illustrated by Forbes (1880a), A-3 seems to be incomplete dorsally and the pessulus is continuous with the dorsal end of A-3L. In other respects Forbes' specimen is similar to mine. In both specimens A-1 through A-6 are fused midventrally.

Psarisomus (Pl. 2) and *Serilophus* are like *Smithornis*, with the following differences. A-1 is divided and closely fitted to A-2, which is complete. At its dorsal end A-1 is broadly spatulate and is twisted so that its internal (concave) surface is directed posteriad. The whole arc of A-1 is at an angle of about 30° with the sagittal plane. A-2 is very narrow laterally but has large, triangular dorsal and ventral surfaces, filling the area between A-1 and the unmodified A-3. At its posterior ends A-2 is continuous with the narrow pessulus.

Lowe's description of *Pseudocalyptomena* suggests a strong similarity to *Psarisomus*. He found some fusion of "the last two or three tracheal rings," probably A-2 through A-4. The pessulus was fused to A-2.

Calyptomena (Pl. 2) is different from the other broadbills. A-1 through A-3 are divided and A-4 is incomplete ventrally. The four elements are fused dorsally to a broad plate extending ventrally into the interbronchial region as a wide pessulus. The posterior borders of this plate are soft white cartilage and blend gradually into the internal tympaniform membranes.

Musculature.

My two specimens of *Smithornis* differ only slightly in their musculature. M. tracheolateralis inserts on the lateral surface of A-5 in *S. capensis*, and on the ventrilateral surface pf A-4 in *S. rufolateralis*. In *S. sharpei* Bates (1914, p. 496) noted that the muscle "goes as far as the bronchus," presumably meaning A-2, the most anterior divided element. Lowe (1924, p. 280) stated that "no muscles could be made out attached to the lower end of the trachea or the bronchi" and Verheyen agreed with him.

M. sternotrachealis was hardly mentioned by the above authors. In *S. capensis* it extends through the center of M. tracheolateralis and is continuous with the deep fibers of the latter. In *S. rufolateralis* it is the superficial fibers of the dorsal half of M. tracheolateralis with which M. sternotrachealis is continuous.

In *Eurylaimus* the insertion of M. tracheolateralis is on the center of A-2. In *Psarisomus, Serilophus* and *Calyptomena* it inserts midlaterally on A-1. In *Cymbirhynchus* the insertion is by a broad tendon to the center of B-1. The fibers of the muscle end at A-2, but when the muscle is lifted the tendon becomes evident. Forbes' description and illustration of this muscle inserting on A-2 are probably in error. Of *Corydon sumatranus,* Müller stated only that muscles are lacking on the lower trachea, implying a condition like that of *Smithornis*. In *Pseudocalyptomena* Lowe described a pair of "intrinsic muscles," apparently inserting on A-1. It is evident from the description and the accompanying illustration that this pair are the Mm. tracheolaterales, and that there are no intrinsic muscles in the usual sense.

M. sternotrachealis is more variable in its form of insertion. In *Eurylaimus* it is wholly continuous with M. tracheolateralis, which it meets at A-8. In *Serilophus* the anterior fibers of M. sternotrachealis are continuous with the superficial ones of M. tracheolateralis and the posterior fibers insert directly on A-11 and A-12. In *Psarisomus,* M. sternotrachealis divides into two fasciculi, which insert directly on A-10 and A-11 at the ventral and dorsal edges of M. tracheolateralis, respectively. In *Calyptomena* the right muscle is similar to that of *Psarisomus,* inserting on A-9 and A-10; the left extends intact through a split in M. tracheolateralis to insert directly on the same elements. In *Cymbirhynchus* the insertion of M. sternotrachealis covers a circular area on A-8 and A-9, adjacent to the dorsal edge of M. tracheolateralis.

SUBORDER TYRANNI.

SUPERFAMILY FURNARIOIDEA.

NOMENCLATURE.

The nomenclature listed on p. 14 applies here, with the following additions:

1) Cartilaginous elements.

Processus vocalis. A cartilaginous or partly ossified plate covering part of the lateral surface of the posterior trachea, anchored by fusion or by fibrous connective tissue to the lower A-elements. It frequently has projecting "horns" (the *processi musculares* of Müller, 1847) to which muscles are attached.

2) Membranes.

Membrana trachealis. This is a membranous window on the ventral and/or dorsal surface of the trachea. It is differentiated from the other membranes of the trachea by the fact that it spans the positions of several elements. The Membrana trachealis may be crossed by narrow sections of several A-elements. In such cases the Membrana trachealis may be considered to be the sum of the series of smaller membranes.

3) Muscles.

M. vocalis ventralis. This name was applied by Rüppell (1933) to the ventral intrinsic muscle of *Lepidocolaptes fuscus.* It originates on the lateral surface of one or more elements anterior to the Membrana trachealis and inserts on the Processus vocalis or on the elements ventral or lateral to the Membrana trachealis.

M. vocalis dorsalis. Rüppell (1933) applied this name to the muscle which occupies a dorsal position corresponding to that of M. vocalis ventralis. It originates on the lateral surface of one or more elements anterior to the Membrana trachealis and inserts on the Processus vocalis or on the elements dorsal or lateral to the Membrana trachealis.

FAMILY DENDROCOLAPTIDAE. WOODCREEPERS.

Specimens Examined.

Of 50 species in 13 genera, I have examined 14 specimens belonging to the following 12 species in nine genera.

Dendrocincla fuliginosa (Vieillot)
Sittasomus griseicapillus (Vieillot)
Glyphorhynchus spirurus (Vieillot), two specimens

Drymornis bridgesii (Eyton)
Xiphocolaptes promeropirhynchus (Lesson)
Xiphocolaptes major (Vieillot)
Dendrocolaptes platyrostris Spix
Xiphorhynchus picus (Gmelin), two specimens
Lepidocolaptes souleyetii (Des Murs)
Lepidocolaptes affinis (Lafresnaye)
Lepidocolaptes albolineatus (Lafresnaye)
Campylorhamphus trochilirostris (Lichtenstein)

I know of only the following descriptions by previous authors:

Dendrocolaptes certhia (Boddaert) — Müller (1847, p. 43; Pl. 6, fig. 12; 1878, p. 35)
Lepidocolaptes fuscus (Vieillot) — Müller (1847, p. 43; 1878, p. 35)
Lepidocolaptes fuscus (Vieillot) — Rüppell (1933, p. 470)

Cartilaginous Elements.

In all the woodcreepers examined the syrinx is dorsoventrally as well as bilaterally symmetrical. In *Dendrocincla* A-1, A-2, and A-3 are divided; A-4, A-5, and A-6 are complete and extremely narrow dorsally and ventrally but of the same width as other elements in the lateral sections. The Membranae tracheales are limited by A-3 and A-7. A-7 and the elements anterior to it are complete and of uniform width. All the B-elements are divided. There are neither a pessulus nor internal cartilages. The Processi vocales are firmly fused to the lateral surfaces of A-1, A-2 and A-3. Well developed horns extend toward the dorsal and ventral midlines in the region of the A-5/A-6 membranes. The most anterior part of the Processus is a round area where M. sternotrachealis inserts, at the level of A-7.

Lepidocolaptes and *Sittasomus* are like *Dendrocincla*, differing as follows. Only A-1 and A-2 are divided; A-3 through A-7 are narrow dorsally and ventrally. The Membranae tracheales extend from A-2 to A-8. A-8 through A-12 are fused into a rigid drum in *Sittasomus* and in *L. souleyetti;* A-8 through A-13 in *L. affinis;* and A-8 through A-14 in *L. albolineatus*. In *L. fuscus* Rüppell reported no fusion and indicated none in his illustration.

Glyphorhynchus is like *Dendrocincla*, differing as follows. A-4 is divided and not narrow. A-5 through A-9 are narrow, the Membranae tracheales extending from A-4 to A-10. In YPM 1802 the drum is formed of A-10 through A-16, but in YPM 1071 it comprises only A-10 through A-13. The horns of the Processus vocalis extend only slightly beyond the main part of the plate.

Xiphocolaptes is like *Dendrocincla*, differing as follows. Only A-1 and A-2 are divided. In *X. major* the Membranae tracheales are like those of *Dendrocincla* but lack the narrow elements extending across them. The drum has the same proportions as that of *Dendrocincla* but fusion is so complete that one cannot count the elements. In *X. promeropirhynchus* the Membranae tracheales extend from A-3 to A-7. The drum consists of A-7, A-8, and A-9.

Campylorhamphus (Pl. 2), *Xiphorhynchus* and *Dendrocolaptes* are like *Xiphocolaptes major*, differing as follows. The drum of *Campylorhamphus* is longer, about nine elements (probably A-10 through A-18) completely fused except for the anterior two. The Membranae tracheales are proportionately shorter than those of *X. major*. In *Xiphorhynchus* the drum comprises six elements (probably A-10 through A-15) incompletely fused. In *Dendrocolaptes* it appears to be A-9 through A-14.

Drymornis differs from all of the others, principally in the form of the Processi vocales. They are completely fused to A-2 and A-1, both of which are divided. The pair of large components thus formed meets at the dorsal and ventral midlines but articulates freely. The Membranae tracheales are free of cross-elements so that one cannot tell how many elements they span. They are longer and narrower than those of other members of the family. The drum consists of three or four elements, completely fused.

Musculature.

The musculature is the same in all of the woodcreepers examined, with minor variations. M. tracheolateralis extends along the lateral surface of the trachea to insert on the lateral surface of the drum, near its anterior edge. *Dendrocincla* is an exception, there being no drum; the insertion is on A-9. In *Xiphocolaptes promeropirhynchus* the insertion is along a spiral line from A-11 ventrally to A-15 dorsally. In *Glyphorhynchus* the muscle divides into two short fasciculi, which diverge to insert on the ventrilateral and dorsolateral surfaces of the drum.

M. sternotrachealis inserts directly on the anterior quarter of the Processus vocalis in all species.

M. vocalis ventralis and M. vocalis dorsalis show little variation among my specimens. They originate on the lateral surface of the drum, immediately posterior to the insertion of M. tracheolateralis and extend posteroventrally and posterodorsally, respectively, to insert on the ventral and dorsal horns of the Processus vocalis. In my specimen of *Xiphocolaptes promeropirhynchus* a narrow band of the superficial fibers of the right M. vocalis ventralis originates at the dorsal edge of M. tracheolateralis, extends across the latter and across the anterior end of M. vocalis dorsalis to join the rest of M. vocalis ventralis. This is probably an individual variant.

FAMILY FURNARIIDAE. OVENBIRDS.

Specimens Examined.

Of 210 species in 55 genera, I have examined the following 29 individuals in 25 species and 22 genera:

Geositta cunicularia (Vieillot), three specimens
Furnarius leucopus Swainson
Cinclodes patagonicus (Gmelin), two specimens
Cinclodes fuscus (Vieillot)
Upucerthia dumetaria Geoff. Saint Hilaire
Limnornis curvirostris Gould
Aphastrura spinicauda (Gmelin)
Phleocryptes melanops (Vieillot), two specimens
Synallaxis cinerascens Temminck
Certhiaxis cinnamomea (Gmelin)
Asthenes pyrrholeuca (Vieillot)
Phacellodomus rufifrons (Wied)

Phacellodomus striaticollis (Lafr, and D'Orb.)
Anumbius anumbi (Vieillot)
Pseudocolaptes boissoneautii (Lafresnaye)
Pseudoseisura lophotes (Reichenbach)
Pseudoseisura gutteralis (Lafr. and D'Orb.)
Anabazenops fuscus (Vieillot)
Philydor rufus (Vieillot)
Automolus ochrolaemus (Tschudi)
Heliobletus contaminatus Berlepsch
Xenops minutus (Sparrman)
Megaxenops parnaguae Reiser
Pygarrhicus albogularis (King)
Sclerurus guatemalensis (Hartlaub)

I know of only the following descriptions in literature:

Cinclodes nigrofumosus (Cabanis) — Müller (1847, p. 42; Pl. 2, fig. 10; 1878, p. 34)
Furnarius rufus (Gmelin) — Müller (1847, p. 41; Pl. 2, figs. 6, 7; 1878, p. 34)
Furnarius leucopus Swainson — Müller (1847, p. 41; Pl. 2, figs. 8, 9; 1878, p. 34)
Xenoctistes rufosuperciliatus (Lafresnaye) — Müller (1847, p. 42; 1878, p. 34)
Heliobletus contaminatus Berlepsch — Müller (1847, p. 42; 1878, p. 34)
Xenops rutilus Lichtenstein — Müller (1847, p. 43; 1878, p. 35)
Sclerurus fuscus Wied — Müller (1847, p. 42; 1878, p. 35)

Cartilaginous Elements.

The configurations of the cartilages in the Furnariidae examined are summarized in Table 1. Although A-1 and A-2 are uniformly divided, the configurations of other A-elements, of the Membranae tracheales, of the drum, and of the Processi vocales show wide variations. Only the examination of a greater series of individuals and species will permit accurate evaluation of variation. The cartilages of the present 25 species may be summarized as follows:

1) A-1, A-2 and all B-elements are divided.
2) A-3 may be of any configuration except double.
3) A-4 is complete in all except *Synallaxis,* in which it is incomplete dorsally.
4) A-5 and subsequent elements are complete.
5) There are neither a pessulus nor internal cartilages.
6) The Processi vocales are narrow flat bars, usually fused posteriorly to the lateral surfaces of A-1 through A-3. In *Cinclodes* they are fused to A-1 and A-2 only; in *Certhiaxis, Asthenes, Phacellodomus,* and *Automolus* to A-1 through A-4; in *Anumbius* and *Pygarrhicus* to A-2 and A-3 only. In all cases the Processi are connected to the A-elements adjacent to them by elastic connective tissue.
7) Dorsal and ventral horns are present on the Processi vocales only in *Geositta.* No intermediates were found between the prominent horns of *Geositta* and the narrow Processi of the other furnariids.
8) In about half of the species examined the Membranae tracheales are limited posteriorly by A-3, the highest numbered posterior limit being A-6 (*Asthenes*).

The anterior limit varies from A-8 (*Limnornis*) to A-15 (*Automolus*) and does not appear to be correlated with the posterior limit. In other words, the Membranae tracheales consist of from five (*Limnornis* and *Asthenes*) to ten (*Anabazenops* and *Automolus*) smaller membranes. Rarely, the dorsal and ventral Membranae may differ in size (*Aphastrura, Synallaxis, Pygarrhicus*).

9) In the majority of cases all of the elements within the limits of the Membranae tracheales cross the Membranae dorsally and ventrally. Within the Membranae each element is about one-third the width of the unmodified A-elements. In the five cases in which crossbars are lacking (*Cinclodes fuscus, Synallaxis, Certhiaxis, Phacellodomus,* and *Pseudoseisura*) they are absent from the anterior halves of the Membranae only and are widest near the posterior limits.

10) In all but four genera two or more elements immediately anterior to the Membranae tracheales are fused, forming a rigid drum. The number of elements varies from two (*Cinclodes fuscus* and *Megaxenops*) to five (*Limnornis* and *Aphastrura*). Fusion may be complete or partial.

Müller's descriptions agree with the above in all essential points.

Musculature.

In all specimens M. tracheolateralis extends along the lateral surface of the trachea to insert on the anterior edge of the drum or, in the absence of a drum, on the element immediately anterior to the Membranae tracheales. M. sternotrachealis inserts on the anterior end of the Processus vocalis. M. vocalis ventralis originates on the ventrilateral surface of the drum or on the element immediately anterior to the Membranae. It extends ventral to the insertion of M. sternotrachealis and inserts directly on the Processus vocalis. The precise region of insertion is variable. The anterior extreme is in *Sclerurus*, in which it inserts just ventral to the insertion of M. sternotrachealis. The most posterior insertion is in *Furnarius* in which it attaches to the base of the Processus, with a few medial fibers attached to A-2. M. vocalis dorsalis originates on the same element or elements as M. vocalis ventralis, immediately dorsal to the latter, and extends dorsal to the insertion of M. sternotrachealis to attach to the surface of the Processus or, in *Furnarius* only, entirely to A-2. In *Geositta* both of the Mm. vocales insert on the ends of the respective horns of the Processi. In most ovenbirds the dorsal and ventral muscles are of equal length, but in *Helioblетus* M. vocalis ventralis inserts on the Processus at the level of A-5 and M. vocalis dorsalis at the level of A-2.

Müller's descriptions agree closely with the above.

FAMILY FORMICARIIDAE. ANTBIRDS.

Specimens Examined.

Of 234 species in 52 genera (including *Conopophaga* Vieillot[1]), I have examined the following 51 individuals of 33 species in 26 genera:

Cymbilaemus lineatus (Leach), two specimens
Hypoedaleus guttatus (Vieillot)
Taraba major (Vieillot)

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[1] *Conopophaga* is included in this family following the conclusions of Ames et al. (1968).

TABLE 1. Configuration of the syringeal cartilages in the Furnariidae.

					Membranae tracheales		Crossbars	Drum	Processi
Genus	A-1	A-2	A-3	A-4	ventr.	dors.	ventr.? dors.?	consists of;	att. to:
Geositta	div.	div.	div.	comp.	A-3 - A-12	same	both	none	A-1 - A-3
Furnarius	div.	div.	i.d.	comp.	A-3 - A-11	same	both	A-11 - A-13	A-1 - A-3
Cinclodes									
patagonicus	div.	div.	div.	comp.	A-3 - A-11	same	both	A-11 - A-13	A-1 - A-2
fuscus	div.	div.	i.v.	comp.	A-3 - A-10	same	neither	A-10 - A-11	A-1 - A-2
Upucerthia	div.	div.	i.v.	comp.	A-3 - A-11	same	both	A-10 - A-12	A-1 - A-3
Limnornis	div.	div.	div.	comp.	A-3 - A-8	same	both	A-8 - A-12	A-1 - A-3
Aphastrura	div.	div.	div.	comp.	A-4 - A-10	A-3 - A-10	both	A-10 - A-14	A-1 - A-3
Phleocryptes	div.	div.	comp.	comp.	A-3 - A-12	same	both	A-12 - A-14	A-1 - A-3
Synallaxis	div.	div.	comp.	i.d.	A-4 - A-11	A-3 - A-11	neither	A-11 - A-12	A-1 - A-3
Certhiaxis	div.	div.	comp.	comp.	A-4 - A-12	same	neither	A-12 - A-15	A-1 - A-4
Asthenes	div.	div.	div.	comp.	A-16 - A-11	same	both	none	A-1 - A-4
Phacellodomus	div.	div.	div.	comp.	A-5 - A-11	same	neither	A-11 - A-12	A-1 - A-4
Anumbius	div.	div.	div.	comp.	A-5 - A-12	same	both	A-12 - A-14	A-2 - A-3
Pseudocolaptes	div.	div.	comp.	comp.	A-3 - A-9	same	both	A-9 - A-12	A-1 - A-3
Pseudoseisura									
lophotes	div.	div.	i.v.	comp.	A-3 - A-11	same	neither	A-11 - A-13	A-1 - A-3
gutteralis	div.	div.	div.	comp.	A-3 - A-11	same	neither	A-11 - A-14	A-1 - A-3
Anabazenops	div.	div.	i.d.	comp.	A-3 - A-13	same	both	A-13 - A-15	A-1 - A-3
Philydor	div.	div.	div.	comp.	A-4 - A-11	same	both	A-11 - A-13	A-1 - A-3
Automolus	div.	div.	i.d.	comp.	A-5 - A-15	same	both	none	A-1 - A-4
Heliobletus	div.	div.	comp.	comp.	A-4 - A-11	same	both	A-11 - A-14	A-1 - A-3
Xenops	div.	div.	div.	comp.	A-3 - A-9	same	both	A-9 - A-12	A-1 - A-3
Megaxenops	div.	div.	i.v.	comp.	A-3 - A-12	same	both	A-12 - A-13	A-1 - A-3
Pygarrhicus	div.	div.	div.	comp.	A-4 - A-10	A-3 - 3-10	both	A-11 - A-13	A-2 - A-3
Sclerurus	div.	div.	comp.	comp.	A-3 - A-11	same	both	none	A-1 - A-3

Sakesphorus canadensis (Linnaeus)
Thamnophilus doliatus (Linnaeus), two specimens
Thamnophilus punctatus (Shaw), three specimens
Thamnophilus caerulescens Vieillot
Pygiptila stellaris (Spix)
Dysithamnus mentalis (Temminck), two specimens
Thamnomanes caesius (Temminck)
Myrmotherula cherriei Berlepsch and Hartert
Myrmotherula axillaris (Vieillot), three specimens
Herpsilochmus pileatus (Lichtenstein)
Microrhopias quixensis (Cornalia)
Neorhopias [= *Formicivora*]*grisea* (Boddaert)
Neorhopias [= *Formicivora*] *rufa* (Wied)
Drymophila squamata (Lichtenstein)
Cercomacra tyrannina (Sclater), two specimens
Pyriglena leucoptera (Vieillot)
Hypocnemis flavescens (Sclater)
Hypocnemoides melanopogon (Sclater)
Myrmeciza exsul Sclater
Myrmoderus squamosus (Pelzeln)
Formicarius analis (Lafr. and D'Orb.), four specimens
Chamaeza brevicauda (Vieillot)
Pithys albifrons (Linnaeus)
Gymnopithys bicolor (Lawrence)
Hylophylax naevioides (Lafresnaye), two specimens
Grallaria varia (Boddaert)
Grallaria perspicillata Lawrence, two specimens
Grallaria ochroleuca (Wied)
Conopophaga lineata (Wied), four specimens
Conopophaga roberti Hellmayr, three specimens

I know of only the following descriptions by previous authors:

Hypoedaleus guttatus (Vieillot) — Müller (1847, p. 39; Pl. 2, figs. 3, 4; 1878, p. 31)
Sakesphorus cristatus (Wied) — Müller (1847, p. 39; Pl. 2, fig. 2; 1878, p. 31)
Thamnophilus doliatus (Linnaeus) — Müller (1847, p. 39; 1878, p. 31)
Thamnophilus punctatus (Shaw) — Müller (1847, p. 39; 1878, p. 31)
Hypocnemis cantator (Boddaert) — Müller (1847, p. 39; 1878, p. 32)
Chamaeza brevicauda (Vieillot) — Müller (1847, p. 40; 1878, p. 33)
Grallaria guatimalensis Prevost and Des Murs — Garrod (1877)
Conopophaga lineata (Wied) — Forbes (1881)
Conopophaga lineata (Wied) — Ames et al. (1968)
Conopophaga roberti Hellmayr — Ames et al. (1968)
Conopophaga aurita (Gmelin) — Müller (1847, p. 40; Pl. 6, fig. 12; 1878, p. 33)

Cartilaginous Elements.

The cartilages of this group are summarized in Table 2. A detailed description of each genus is beyond the scope of this paper, but the following generalizations may be made:

1) Dorsal and ventral Membranae tracheales are present in all genera. There are two types of Membranae, long and short.
    a) Among the genera examined by me, the long type is found only in *Formicarius, Chamaeza,* and *Grallaria.* The anterior limit of the Membrana is characterized by a gradual transition from narrow to broad elements, the inter-element membranes being successively narrower. In the three genera above only the dorsal Membrana is long, the ventral one being abruptly limited anteriorly.
    b) The short type of Membrana, found in all of the other genera studied, is characterized by an abrupt anterior limit, usually at about A-10. In this case the limiting element often has approximately the same width as all of the elements anterior to it. The element just posterior to the anterior limit is usually the narrowest of those crossing the Membrana.
2) Processi vocales are present in all genera, but are usually small and attached only to those elements within the limits of the Membranae tracheales (see *Taraba,* Pl. 3). Exceptions are the Processi of *Formicarius* (Pl. 3), *Chamaeza* (Pl. 4), *Conopophaga* (Pl. 4) and *Grallaria,* which are broad, thick and long, extending from A-1 or A-2 anteriad in *Formicarius* to A-10, in the various species of *Grallaria* to A-10, A-11 or A-12, in *Chamaeza* to A-17, and in *Conopophaga* to A-9, A-10, A-11 or A-12.
3) The pessulus is absent in all antbirds examined by me or by previous authors.
4) No forms are known possessing internal cartilages.
5) The configuration of the lower A-elements varies among the genera examined (see Table 2). In all specimens A-1 is divided and A-4 complete, the variability being limited to A-2 and A-3. The differences between A- and B-elements are less pronounced in this family than in others of the Furnarioidea. All of the B-elements are divided. Some are partly ossified and in many the plane of curvature is nearly perpendicular to the bronchial axis.

Musculature.

In syringeal musculature the family is sharply divided into two categories, which may be summarized as follows:

1) *Formicarius* (Pl. 3), *Chamaeza* (Pl. 4), *Grallaria* and *Conopophaga* (Pl. 4). M. tracheolateralis is variable in this group. In *Formicarius, Grallaria* and *Conopophaga* it is a narrow lateral band; in *Chamaeza* a broad ventrilateral one. Insertion in *Formicarius* and *Grallaria* is entirely on the anterior end of the Processus vocalis, except in YPM 1068 (*G. perspicillata*), in which the ventral fifth of the muscle inserts on A-10. In *Chamaeza* the ventral three-quarters of the fibers are attached to A-16 through A-18 and the lateral quarter of them to the Processus. In *Conopophaga* the fibers at the dorsal and ventral edges insert on A-10, A-11 and A-12, the remainder usually being continuous with M. sternotrachealis. In individuals with long Processi, the deep fibers insert on the anterior end of the Processus.

    In *Formicarius, Chamaeza* and *Grallaria,* M. sternotrachealis inserts wholly on the anterior end of the Processus, except in YPM 1068, in which the anterior fibers of M. sternotrachealis are continuous with the super-

TABLE 2. Configuration of the syringeal cartilages in the Formicariidae.

Genus	A-1	A-2	A-3	A-4	*Membranae tracheales* ventral	*Membranae tracheales* dorsal	*Processi vocales* attached to:
Cymbilaemus	div.	div.	i.d.	compl.	A-3 - A-9	A-4 - A-10	A-4 - A-9
Hypoedaleus	div.	div.	i.d.	comp.	A-3 - A-9	A-4 - A-9	A-4 - A-8
Taraba	div.	div.	comp.	comp.	A-2 - A-10	A-3 - A-11	A-2 - A-8
Sakesphorus	div.	div.	comp.	comp.	A-3 - A-9	A-3 - A-12	A-3 - A-4
Thamnophilus							
caerulescens	div.	i.d.	comp.	comp.	A-3 - A-9	same	A-5 - A-9
doliatus	div.	div.	comp.	comp.	A-3 - A-9	same	A-4 - A-8
punctatus	div.	div.	i.d.	comp.	A-3 - A-9	same	A-5 - A-8
Pygiptila	div.	div.	comp.	comp.	A-3 - A-12	same	A-6 - A-9
Dysithamnus	div.	comp.	comp.	comp.	A-2 - A-9	A-2 - A-10	A-2 - A-7
Thamnomanes	div.	i.d.	comp.	comp.	A-3 - A-9	A-1 - A-9	A-2 - A-8
Myrmotherula	div.	div.	comp.	comp.	A-3 - A-8	A-3 - A-9	A-4 - A-8
Herpsilochmas	div.	div.	i.d.	comp.	A-3 - A-10	A-2 - A-12	A-3 - A-8
Microrhopias	div.	div.	comp.	comp.	A-5 - A-10	A-3 - A-8	A-4 - A-8
Neorhopias	div.	i.d.	comp.	comp.	A-2 - A-9	A-4 - A-9	A-4 - A-6
	(div. A-2aR present)						
Drymophila	div.	div.	i.d.	comp.	A-3 - A-9	same	A-5 - A-8
Cercomacra	div.	comp.	comp.	comp.	A-2 - A-9	same	A-3 - A-9
Pyriglena	div.	div.	i.d.	comp.	A-3 - A-11	A-4 - A-12	A-4 - A-9
Hypocnemis	div.	comp.	comp.	comp.	A-4 - A-12	A-3 - A-12	A-4 - A-8
Hypocnemoides	div.	div.	comp.	comp.	A-3 - A-11	same	A-4 - A-7
Myrmeciza	div.	div.	comp.	comp.	A-2 - A-12	A-3 - A-10	A-6 - A-10
Myrmoderus	div.	div.	comp.	comp.	A-4 - A-9	A-3 - A-7	A-4 - A-7
Formicarius	div.	div.	div.	comp.	A-4 - A-10	A-3 - A-11	A- - A-
Chamaeza	div.	div.	i.d.	comp.	A-2 - about A-30*	A-2 - about A-21*	A-2 - A-14
Pithys	div.	div.	i.d.	comp.	A-4 - A-11	A-4 - A-10	A-4 - A-7
Gymnopithys	div.	div.	comp.	comp.	A-2 - A-9	A-2 - A-10	A-4 - A-7
Hylophylax	div.	div.	comp.	comp.	A-4 - A-10	A-3 - A-9	A-4 - A-7
Grallaria	div.	div.	comp.	comp.	A-3 - about A-30*	A-3 - about A-20*	A-4 - A-7
Conopophaga	div.	div.	i.d.	comp.	A-3 - A-11	A-2 - A-13	

*There is no finite anterior limit to the Membranae tracheales in *Chamaeza* and *Grallaria*.

ficial lateral fibers of M. tracheolateralis. In most specimens of *Conopophaga*. M. sternotrachealis is largely continuous with M. tracheolateralis, the deeper fibers inserting on A-10, A-11 and A-12. When the Processus is long the deeper fibers of M. sternotrachealis insert on its anterior end.

There are no intrinsic muscles in any of these genera.

Müller's descriptions of *Chamaeza* and *Conopophaga*, and Garrod's of *Grallaria* agree with the above regarding insertions of the extrinsic muscles and the lack of intrinsic ones. Forbes' description of *Conopophaga* applies only to individuals with short Processi.

2) All other genera of this family examined by me (example: *Taraba*, Pl. 3). M. tracheolateralis inserts ventrally and ventrilaterally on several elements anterior to the Membranae tracheales and sometimes also on the dorsal side of the anterior end of the Processus. M. sternotrachealis characteristically divides into two fasciculi. The posterior one inserts on the anterior end of the Processus, the anterior one on the dorsolateral surfaces of several elements immediately anterior to the Membrana. In some individuals there is fiber continuity between portions of the two extrinsic muscles. The paired intrinsic muscle, which I tentatively call M. vocalis ventralis, originates on the ventral surfaces of several elements immediately anterior to the Membrana. Usually the line of origin is most posteriorly situated near the ventral midline and angles anterolaterally, following the line of insertion of M. tracheolateralis. Extending across the anterior corner of the Membrana, M. vocalis ventralis inserts on the anterior end of the Processus immediately anterior to the insertion of M. sternotrachealis. The precise regions of origin and insertion of the intrinsic muscle vary greatly among the members of this diverse family. Usually the muscle extends between the two fasciculi of M. sternotrachealis.

Most of the characteristics of this second group were noted by Müller in his detailed descriptions of *Hypoedaleus* and *Thamnophilus*.

FAMILY CONOPOPHAGIDAE. ANTPIPITS AND GNATEATERS.

This family was erected by Forbes (1881) for the genera *Conopophaga* and *Corythopis*, on the basis of characters of the syrinx, sternum and tarsus. Ames et al. (1968) reexamined these and other characters in the two genera and compared them with a number of other suboscines, concluding that *Corythopis* must be placed in the superfamily Tyrannoidea and *Conopophaga* returned to the Formicariidae. The reader will find *Conopophaga* at the end of the Formicariidae (p. 26) and *Corythopis* in the subfamily Euscarthminae of the Tyrannidae (p. 66).

FAMILY RHINOCRYPTIDAE. TAPACULOS.

Specimens Examined.

Of 38 species in 12 genera (including *Melanopareia* Reichenbach[1] and *Psilo-*

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[1] The genus *Melanopareia* was placed by Hellmayr (1924) in the Formicariidae, but W. W. Miller (*in* Wetmore, 1926) found that its metasternum has two pairs of notches, suggesting that the genus belongs in the Rhinocryptidae. Peters (1948) agreed with Wetmore and is followed here.

rhamphus Sclater[1]), I have examined the following 10 individuals in eight species and seven genera:

Pteroptochos tarnii (King), two specimens
Pteroptochos megapodius Kittlitz
Scelorchilus rubecula (Kittlitz)
Rhinocrypta lanceolata (Geoff. Saint Hilaire), two specimens
Teledromas fuscus (Scl. and Salv.)
Melanoparcia maximilliani (D'Orbigny)
Scytalopus magellanicus (Gmelin)
Triptorhinus [= *Eugralla*] *paradoxus* (Kittlitz)

I know of only the following descriptions by previous authors:

Pteroptochos megapodius Kittlitz — Garrod (1877)
Scytalopus indigoticus (Wied) — Müller (1847, p. 41; 1878, p. 33)
Psilorhamphus guttatus (Menetries) — Plótnick (1958)

Cartilaginous elements.

Pteroptochos (Pl. 4) is typical of the family. A-1 and A-2 are divided; A-3 is incomplete dorsally; A-4 and subsequent elements are complete. Membranae tracheales are present ventrally and dorsally. The ventral one is limited posteriorly by A-3. Anteriorly the elements become successively wider, attaining a uniform width at about A-27 in *P. megapodius* and about A-20 in *P. tarnii*. The dorsal Membrana is limited abruptly by A-2 posteriorly and by A-14 anteriorly. There are prominent Processi vocales, attached at their broad bases to A-1 and A-2. They are narrow in the region of A-5 through A-9 and broad anteriorly, providing surfaces for muscle attachments. There are neither a pessulus nor internal cartilages.

Garrod's description of *P. megapodius* differed from the above only on minor points. He noted that elements A-3 through A-14, which crossed the Membranae as narrow bands, were incomplete laterally, "as they are in all the Trachaeophonae." In the latter remark Garrod was in error. Whatever the condition in his specimen, the elements crossing the Membranae are usually complete laterally. Removal of the Processi frequently damages the underlying elements, to which the Processi are attached.

Rhinocrypta is like *Pteroptochos,* differing as follows. A-1 is extremely heavy, about twice the width and thickness of elements anterior to the Membranae. A-2 is incomplete dorsally. A-1, A-2, and A-3 are joined ventrally by two narrow medial plates. At the anterior edge of the ventral Membrana A-16 and A-17 are incomplete ventrally and are intermediate in width between A-15 (the narrowest element) and A-18 (as wide as those anterior to it).

Teledromas is like *Pteroptochos*, differing as follows. Both Membranae are abruptly limited anteriorly by A-14. The trachea is very broad in the region of A-10 and strongly compressed dorsoventrally. The Processi are robust and extend from A-1 and A-2, to which they are fused, anteriorly to the level of A-13.

Scelorchilus is like *Pteroptochos*, differing as follows. A-3 is complete. The ventral Membrana ends abruptly at A-18 and the dorsal one at A-16.

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[1] *Psilorhamphus* is included in this family, following Plótnick (1958).

Scytalopus is like *Pteroptochos,* differing as follows. A-3 is divided. Both Membranae are limited anteriorly by A-10, which is intermediate in width between A-9 and A-11 dorsally, but has the full width of A-11 ventrally. The Processi vocales are attached to A-2 and A-3 only. Müller's description agrees closely with the above.

Triptorhinus is like *Pteroptochos,* differing as follows. A-3 is complete. The dorsal Membrana is sharply limited by A-1 posteriorly and by A-13 anteriorly, the ventral one by A-2 and A-11. In other words A-2, A-11, and A-12 are narrow dorsally and broad ventrally.

Melanopareia (Pl. 4) is unlike all of the above in several ways. A-1 is divided; A-2 is incomplete dorsally; A-3 and subsequent elements are complete. The anterior limits of both Membranae are gradual, A-8 and A-9 being intermediate in width between A-7 and A-10. A rigid drum is formed by the fusion of A-10 through A-12 and, dorsally, through A-14. The Processi vocales are broad plates without constrictions. They are attached by fibrous connective tissue to A-2 through A-7. The maximum width of the trachea, at A-7, is about twice that where the width is uniform, anterior to A-14.

In describing the syrinx of *Psilorhamphus,* Plótnick did not mention details of the cartilages, but it appears from his illustration (showing only the dorsal view) that A-1 and A-2 are divided or incomplete dorsally. The dorsal Membrana evidently is rather short, being limited by A-2 and A-10.

Musculature.

In *Pteroptochos* (Pl. 4) M. tracheolateralis extends down the lateral surface of the trachea to insert on the anterior end of the Processus vocalis, with a few ventral fibers attached to A-16. M. sternotrachealis also inserts on the Processus, immediately posterior to M. tracheolateralis and partly surrounded by it. A thin, narrow intrinsic muscle, for which I tentatively use the name M. vocalis dorsalis, originates on A-16 adjacent to the dorsal fibers of M. tracheolateralis and spirals posteroventrally across the surface of the latter muscle to insert on the Processus just ventral to the insertion of M. tracheolateralis. The intrinsic muscle is more strongly developed in *P. tarnii* than in *P. megapodius.*

Garrod's description of *P. megapodius* was almost entirely devoted to cartilaginous elements. He mentioned the insertions of M. sternotrachealis and M. tracheolateralis on the Processus, but neither described nor illustrated an intrinsic muscle.

Scelorchilus is like *Pteroptochos,* differing as follows. M. tracheolateralis divides into two fasciculi at the level of A-19. The fasciculi insert on the anterior end of the Processus on either side of the insertion of M. sternotrachealis. The latter also divides into two fasciculi near its insertion: a dorsolateral one inserting on the Processus vocalis and on the lateral surfaces of A-16 through A-18 and a ventral fasciculus which inserts on the ventrilateral surfaces of A-16 through A-18 adjacent to M. tracheolateralis. M. vocalis dorsalis originates on the dorsolateral surfaces of A-13 through A-17 and extends superficial to the two extrinsic muscles to insert on the ventral edge of the Processus.

Triptorhinus is like *Pteroptochos,* differing as follows. M. tracheolateralis inserts along a spiral line from the lateral region of A-13 to the dorsolateral region of A-19. A narrow ventral fasciculus inserts on the ventrilateral surfaces of A-13 and A-14.

M. vocalis dorsalis originates on the dorsal surfaces of A-14 through A-23 and spirals posterolaterally to insert on the Processus vocalis.

Melanopareia (Pl. 4) is like *Pteroptochos,* differing as follows. M. tracheolateralis inserts on the ventral side of the Processus vocalis adjacent to the insertion of M. sternotrachealis. M. vocalis dorsalis originates on the dorsal surfaces of A-10 through A-12. Its insertion covers most of the ventrilateral surface of the Processus, from A-3 to A-6, where it is in contact with the insertion of M. tracheolateralis.

Rhinocrypta is like *Pteroptochos,* differing as follows. M. tracheolateralis divides into two fasciculi, a narrow dorsal one inserting on A-16 and a broad ventral one inserting on A-19 and A-20. M. vocalis dorsalis originates on the dorsolateral surfaces of A-17 through A-22. Its fibers are parallel to those of the ventral branch of M. tracheolateralis. The insertion is on the Processus, ventrally adjacent to the insertion of M. sternotrachealis.

Scytalopus is unlike all of the above. M. tracheolateralis inserts dorsolaterally in a broad area of A-11 and A-12 and laterally on the Processus vocalis. Some superficial dorsolateral fibers are continuous with part of M. sternotrachealis, the remainder of which inserts on the Processus. The intrinsic muscle consists of a narrow band of fibers nearly covered by M. tracheolateralis. It originates on the lateral surface of A-19 and inserts on the anterior end of the Processus. Without more specimens I am unwilling to name this muscle in the terms applied to those of other rhinocryptids. Müller mentioned the insertion of M. sternotrachealis on the Processus and stated without further description that the Processus is drawn upward by "other muscles."

Teledromas is unlike all of the above. M. tracheolateralis is a narrow lateral band inserting on the anterior end of the Processus vocalis. M. sternotrachealis inserts in a circular area of the Processus, immediately posterior to the insertion of M. tracheolateralis. There are no intrinsic muscles.

In *Psilorhamphus* Plótnick found one pair of intrinsic muscles, which he described as extensions of the Mm. tracheolaterales, "as in many birds." It is evident from the illustration that both the intrinsic muscle and M. tracheolateralis insert on the anterior end of the Processus, but I cannot make out whether the intrinsic muscle lies posterior or ventral to the extrinsic one. The origins of the muscles are not shown. M. sternotrachealis (called "costo-tracheal" by Plótnick) inserts directly on the anterior end of the Processus.

SUPERFAMILY TYRANNOIDEA.

NOMENCLATURE.

The nomenclature on p. 14 is applicable to this suborder, with the following additions:

1) Cartilaginous elements.

Internal cartilages. This term was applied by Miskimen (1963) to the paired cartilaginous plates lying in the internal tympaniform membranes. Müller's (1847) term *Cartilago arytenoidea* implies homology to the arytenoid cartilages of the mammalian larynx and hence is not appropriate. Internal cartilages are variable in shape and in number and may float freely in the membranes or be attached to other elements.

2) Muscles.

M. obliquus ventralis is a new name for the paired intrinsic muscle originating directly or on a median raphe at or near the ventral midline. It extends posterolaterally, to insert on one or more elements or on the membranes between them. This muscle was first named by Miskimen (1963), but the name that she used, "M. syringeoventralis", is much like the name "M. syringeus ventralis," applied by Setterwall (1901) and others to one of the oscine syringeal muscles. To avoid misunderstanding a wholly new name appears justified. Müller applied the term "kehlkopfmuskel" to this and all other intrinsic syringeal muscles.

M. obliquus lateralis is a new name for another paired intrinsic muscle that originates on the lateral surface of one or more A-elements and extends posteriorly or posteroventrally to insert on one or more elements, usually near the insertion of M. obliquus ventralis. Miskimen (1963) called this "M. syringeo-lateralis."

M. obliquus dorsalis originates on or near the dorsal midline and extends posterolaterally to insert on one or more A- or B-elements. It has not been described by previous authors.

FAMILY COTINGIDAE. COTINGAS.

Specimens Examined.

Of 92 species in 34 genera (including *Pseudattila* Zimmer 1936, *Zaratornis* Koepke 1954, and *Conioptilon* Lowery and O'Neill 1966), I have examined the following 39 individuals of 30 species in 23 genera:

Phoenicircus carnifex (Linnaeus)
Heliochera rubrocristata (Lafr. and D'Orb.)
Cotinga amabilis Gould
Cotinga maculata (Müller)
Xipholena punicea (Pallas)
Carpodectes nitidus Salvin
Euchlornis jucunda (Sclater)
Euchlornis aureopectus (Lafresnaye), two specimens.
Iodopleura isabellae (Shaw and Nodder)
Attila spadiceus (Gmelin)
Attila cinnamomeus (Gmelin)
Casiornis rufa Vieillot
Laniocera rufescens (Sclater)

Rhytipterna holerythra (Scl. and Salv.), three specimens.
Lipaugus unirufus Sclater
Pachyramphus rufus (Boddaert)
Pachyramphus polychopterus (Vieillot), two specimens
Pachyramphus viridis (Vieillot)
Platypsaris aglaiae (Lafresnaye), three specimens
Tityra semifasciata (Spix)
Tityra inquisitor (Lichtenstein)
Tityra cayana (Linnaeus)
Querula purpurata (Müller)
Pyroderus scutatus (Shaw), two specimens
Cephalopterus ornatus Geoff. Saint Hilaire
Perissocephalus tricolor (Müller)
Gymnoderus foetidus (Linnaeus)
Conioptilon mcilhennyi Lowery and O'Neill
Procnias tricarunculata (J. and E. Verreaux)
Rupicola rupicola (Linnaeus), three specimens

I know of the following descriptions by previous authors:

Phibalura flavirostris Vieillot — Müller (1847, p. 32; 1878, p. 26)
Xipholena punicea (Pallas) — Müller (1847, p. 31; Pl. 6, figs. 1, 2; 1878, p. 26)
Iodopleura pipra (Lesson) — Müller (1847, p. 30; 1878, p. 25)
Calyptura cristata (Vieillot) — Müller (1847, p. 30; 1878, p. 25)
Lipaugus cineraceus (Vieillot) — Garrod (1877b)
Pachyramphus rufus (Boddaert) — Müller (1847, p. 32; Pl. 6, fig. 6; 1878, p. 26)
Platypsaris aglaiae (Lafresnaye) — Garrod (1877b)
Tityra cayana (Linnaeus) — Müller (1847, p. 31; Pl. 6, fig. 5; 1878, p. 26)
Pyroderus scutatus (Shaw) — Garrod (1878)
Cephalopterus ornatus Geoff. Saint Hilaire — Tschudi (1843)
Cephalopterus ornatus Geoff. Saint Hilaire — Sick (1954)
Perissocephalus tricolor (Müller) — Müller (1847, p. 31; Pl. 6, fig. 4; 1878, p.26)
Conioptilon mcilhennyi Lowery and O'Neill — Lowery and O'Neill (1966)
Procnias alba (Hermann) — Müller (1847, p. 26; Pl. 1, figs. 1-6; 1878, p. 22)
Procnias nudicollis (Vieillot) — Müller (1847, p. 27; Pl. 1, figs. 8-14; 1878, p. 23)
Rupicola rupicola (Linnaeus) — Müller (1847, p. 31; Pl. 6, fig. 3; 1878, p. 26)

Cartilaginous Elements.

In *Cotinga* (Pls. 15 and 16) A-1 is divided; A-2 is double; A-3 is divided; A-4 is incomplete ventrally; A-5 and subsequent elements are complete. Each element has a thin flange at its posterior edge overlapping the anterior edge of the next element. The pessulus is fused to A-4 at the dorsal midline. At its ventral end it is connected to A-3 and A-4 by cartilaginous strips. There are no internal cartilages. All of the B-elements are divided. The middle third of B-1 is enclosed in a mass of fibrous connective tissue, some of which is attached to A-1 and B-2.

Xipholena is like *Cotinga,* differing as follows. A-1 through A-4 are divided. The pessulus is fused dorsally to both A-4 and A-5 and ventrally to A-5. There is no fibrous connective tissue enclosing B-1. Müller's description and illustration of *Xipholena* agree closely with the above.

Conioptilon is like *Cotinga,* differing as follows. A-1 through A-4 are divided and there is an extra component, A-3aL. The elements lack the flanges found in *Cotinga.* The pessulus is fused to A-4 at both ends. B-1 is only slightly curved and is not enclosed in connective tissue. Lowery and O'Neill (1966), whose information was provided by me from the specimen described here, were concerned only with the general similarity of the syrinx of *Conioptilon* to those of the Cotinginae and Gymnoderinae.

Phoenicircus is like *Cotinga,* differing as follows. A-1 through A-4 are divided. A-1 is ossified only for the dorsal quarter, but this may be individually variable. The element is quite narrow and is straighter than A-2. The pessulus ends dorsally in a small plate which lies between the ends of A-3 and A-4. At the ventral end it butts with the ends of A-3. The ventral ends of A-3 and A-4 are tightly bound together with fibrous connective tissue. There is no mass of tissue surrounding B-1.

Euchlornis is like *Cotinga,* differing as follows. The two species examined differ slightly from each other. In *E. jucunda* A-1 through A-5 are divided; A-6 and subsequent elements are complete. The pessulus is fused to A-6. In *E. aureopectus* only A-1 through A-3 are divided; A-4 and subsequent elements are complete. The pessulus is fused to A-4 at both ends. In both species B-1 is a very heavy element, bent anteriad at the ends.

Tityra is like *Cotinga,* differing as follows. There are minor variations among the specimens examined. In *T. semifasciata* A-3 is complete and carries the pessulus. There is an extra divided component A-2aR. In *T. inquisitor* A-3 is divided and fused dorsally to A-4, which is complete and bears the pessulus. In *T. cayana* A-1 through A-5 are divided and the pessulus is absent. In all three specimens the anterior ends of the internal tympaniform membranes consist of a continuous sheet of cartilage which is attached to the dorsal and ventral ends of the divided elements, and contains the pessulus. At its edges the sheet blends into connective tissue, which encloses the ends of B-1. Müller's specimen of *T. cayana* was virtually identical to mine, to judge from his illustration.

Heliochera is like *Cotinga,* differing as follows. Only A-1 is divided; A-2 and subsequent elements are complete. The pessulus is fused dorsally and ventrally to A-2. Partial dissection by C. William Beebe has removed the connective tissue surrounding B-1, if any was present.

Of *Phibalura,* Müller (1878, p. 26) stated only that "the thin lateral muscle is inserted into the third bronchial ring," suggesting that probably only the lower two or three A-elements were divided. He described *Calyptura* as like "the true Ampelinae" (Cotinginae) and we may infer from the description that A-1 and possibly A-2 are divided.

Querula is unlike all of the above. The specimen is lacking everything posterior to B-1. A-1 through A-4 are divided and are very broad, each element overlapping the one posterior to it. A-5 is incomplete dorsally; A-6 and subsequent elements are complete. B-1 is divided and narrow. A narrow pessulus is fused to A-6 at both ends. The entire region from A-1 through A-6 consists of a hemispherical chamber, the diameter of which is about twice that of the trachea at A-10.

Carpodectes is like *Querula*, differing as follows. A-1 through A-7 are divided; A-8 and subsequent elements are complete. The ventral ends of B-1 through A-7 are connected by a horseshoe-shaped piece of soft cartilage, the ends of which almost touch at B-1. A similar cartilage joins the dorsal ends of the same elements. The narrow pessulus is fused to A-8 at both ends.

Pyroderus is unlike all of the above (see Pl. 20). Immediately behind the larynx the trachea is enlarged, mostly dorsoventrally, forming a long chamber, elliptical in cross section. In the region of A-21 through A-26 the trachea tapers to a circular cross section. A second chamber lies in the region of bifurcation, enclosed by B-1 through A-6. It is more conical in shape than hemispherical. The lateral diameter of the syrinx at A-1 is about three times that at A-10, where the lower trachea is narrowest. A-1 and A-2 are divided; A-3 is incomplete dorsally; A-4 and subsequent elements are complete. A-4 and A-5 are broadly fused at the dorsal and ventral midlines, as are A-5 and A-6. A-3 and A-4 are fused at the ventral midline only. The broad, heavy pessulus is fused to A-3 at the ventral end only. The posterior ventral edge of A-3 has a deep semicircular indentation on each side of the midline and the anterior ventrilateral edge of A-2 has similar indentations. The two combine to create a pair of roughly circular membranous windows completely bordered by the elements, which are tightly attached to each other by fibrous connective tissue at the edges of the windows. The posterior lateral edge of A-1 has a shelf-like extension projecting well beyond B-1. There are only six B-elements, all of them divided. They decrease in size progressively in the posterior direction, resulting in strongly tapered bronchi. Garrod's description and illustrations of the syrinx of *Pyroderus* agree closely with the above.

Perissocephalus is like *Pyroderus*, differing as follows. A-1 through A-4 are divided; A-5 and subsequent elements are complete. The dorsal and ventral fifths of each divided element are soft cartilage, while the middle three-fifths is hard. The soft regions are convex, relative to the lumen. A small semicircular piece of soft cartilage connects the ends of A-1 through A-4, also touching B-1. The lower A-elements in this genus and in those below lack the elaborate sculpturing found in *Pyroderus*.

Müller's description of *Perissocephalus* implied that it is much like *Pyroderus*. He mentioned that A-1 through A-5 are divided and that there is an enlargement of the anterior part of the trachea as in *Cephalopterus*.

Cephalopterus is like *Pyroderus*, differing as follows. A-1 through A-5 are divided; A-6 and subsequent elements are complete. The pessulus (Pl. 21) is fused to A-6 at both ends and is indented to receive the ends of A-5, which fit closely to it. At each midline, where the pessulus meets A-6, there is a triangular hole with the point directed anteriad. There are only four B-elements. They are delicate and successively smaller in diameter. The descriptions of *Cephalopterus* by Tschudi and by Sick were confined to the exterior shapes of the respiratory tubes. Both noted the anterior expansion of the trachea, the chamber in the syringeal region, and the short bronchi.

Gymnoderus is like *Pyroderus*, differing as follows. The trachea is expanded in the region of A-8 through A-19, rather than more anteriorly. The dorsoventral diameter at A-13 is about twice the lateral diameter; at A-5 the ratio of the two diameters is about 1.5 to 1. A-1 through A-3, all divided elements, are arched, concave posteriorly. The pessulus is fused to A-4 at both ends. There are six B-elements, B-1 being heavy and dorsally spatulate, the others being delicate and decreasing in diameter consecutively.

Rupicola is unlike all of the above. A-1 through A-3 are divided; A-4 and subsequent elements are complete. A-4 through A-6 are wholly fused, except for ventrilateral spaces between A-5 and A-6 in the AMNH specimen. The pessulus is fused to A-4 at both ends. B-1 is closely fitted to A-1 from which it differs in shape and hardness. The NYZS specimen was stained with alizarin by Dr. Beebe (using the technique of

Hollister, 1934) in order to determine the degree of calcification of the elements. All of the A-elements were heavily stained, the B-elements virtually not at all. Müller mentioned only the musculature of *Rupicola.*

Procnias is unlike all of the above. A-1 through A-4 are divided and are fused, forming a pair of broad curved plates. The diameter of the syrinx at A-1 is about three times that at A-7. A-5 is a very narrow complete element, the edges of which are closely fitted to adjacent elements. The pessulus appears to float in about the middle of the long space between A-1 and B-1, held in place by the surrounding membranes. The A-1/B-1 membrane is very long anteroposteriorly, about equal to the distance covered by the first six A-elements.

Müller's detailed descriptions of *P. alba* and *P. nudicollis* were primarily concerned with musculature. In the former species he found two divided elements (probably A-1 and A-2) anterior to the long membrane; in the latter species there was only a single divided element there. Possibly the "single" element was composed of several fused elements.

Attila (Pls. 15 and 16) is unlike all of the above. A-1 is divided; A-2 is double; A-3 is divided; A-4 is incomplete dorsally; A-5 and subsequent elements are complete. In YPM 2130 there is an extra divided component, A-3aR. B-1 is heavy and is spatulate dorsally. The pessulus is attached to A-4 ventrally and free dorsally. There are two pairs of internal cartilages. A large ⅃-shaped dorsal pair is fused anteriorly to the medial region of A-2, the short arm of each "⅃" extending ventrad. The other pair float in the ventral part of the internal tympaniform membranes at the level of B-2. Each is a small "⅃" with the corner situated anteriorly and the short arm directed dorsad. The bronchi are long and straight, with very little taper.

Casiornis is like *Attila,* differing as follows. A-3 is incomplete ventrally and A-4 is complete. The pessulus is a soft narrow bar fused dorsally to A-3 and free ventrally. The internal cartilages are more J-shaped than ⅃-shaped, and are about half as wide as in *Attila.* The smaller pair are short straight bars in line with the ventral ends of the larger ones.

Rhytipterna is like *Attila,* differing as follows. The pessulus ends ventrally in a small elliptical plate which fits the space between the ventral ends of A-2 and A-3 but is not fused. The dorsal internal cartilages are much narrower than those of *Attila* and are strongly J-shaped. The ventral pair are small thick bars close to the ventral ends of the dorsal pair.

Laniocera is like *Attila,* differing as follows. A-2 is divided and A-3 is complete. The two elements are fused near the ventral midline. The ventral internal cartilages are short, straight thick bars, flattened on their medial surfaces, where they are in contact with each other.

Iodopleura is unlike all of the above. A-1 is divided; A-2 is incomplete dorsally; A-3 and subsequent elements are complete. The midventral region of A-2 is very broad and blends imperceptibly into the pessulus, which touches the dorsal ends of A-2 but is not fused to them. A pair of very small, short, roughly triangular internal cartilages is fused to the pessulus near the ends of A-2. All of the B-elements are divided. B-1 is shorter and straighter than the others, resulting in markedly constricted bronchi. The latter are long and nearly untapered.

Pachyramphus is unlike all of the above. In *P. rufus* and *P. polychopterus* A-1 is divided; A-2 is incomplete ventrally; A-3 and subsequent elements are complete. There is no flare in the syringeal region, A-1 having about the same diameter as the more anterior elements. In both specimens of *P. polychopterus* the pessulus is fused dorsally to A-2 and is free ventrally; in the specimen of *P. rufus* it is fused ventrally to A-2R; and in *P. viridis* A-2 is complete and bears the pessulus. There is a single pair of very small, straight, narrow, internal cartilages, situated at the dorsal edge of the internal tympaniform membranes. Müller's description of *P. rufus* was concerned only with the musculature.

Platypsaris is like *Pachyramphus*, differing only in that A-2 is divided and the internal cartilages are slightly wider. The pessulus is attached to A-3. Garrod apparently found A-2 to be complete in his specimen. His description does not make clear the position of the A-1/B-1 membrane, for he mentioned (1878, p. 143) the "the second bronchial semi-ring is not modified" (in comparison with the first semi-ring, which is "of the same flattened and deep nature as the tracheal rings"), but that the third semi-ring is "the commencement of the normal bronchus."

Lipaugus is unlike all of the above. A-1 and A-2 are divided; A-3 are subsequent elements are complete. A-2 through A-4 are connected by areas of soft cartilage, creating a semi-rigid drum. The pessulus is fused to A-3 at both ends. The 15 B-elements are of nearly uniform size, resulting in long, straight, only slightly tapered bronchi. The middle three-fifths of each B-element is ossified. B-1 is arched anteriorly and lies close to A-1, with the intervening region filled with fibrous connective tissue. There are no internal cartilages. The syrinx of *L. cineraceus*, as described by Garrod, is identical to that of *L. unirufus*.

Musculature.

In *Cotinga* (Pls. 15 and 16), M. tracheolateralis is a narrow, lateral band which broadens near its insertion to nearly twice its anterior width. It inserts on the connective tissue surrounding B-1. In my specimen of *C. amabilis* a slip from the dorsal edge of the muscle inserts on the dorsolateral surface of A-7 (probably an individual variant). In both species M. sternotrachealis inserts on the dorsolateral surfaces of A-9 through A-14, adjacent to the dorsal edge of M. tracheolateralis. There are no intrinsic muscles.

Xipholena is like *Cotinga*, differing as follows. About the ventral third of the fibers of Mm. tracheolaterales are attached to the trachea at A-8 on the left and at A-9 on the right. The attachment is not readily apparent and seems to involve only the deep fibers of the muscle. M. sternotrachealis inserts on A-12 through A-14.

Euchlornis is like *Cotinga*, differing only in that M. tracheolateralis is proportionately twice as wide and M. sternotrachealis is continuous with the dorsal superficial fibers of M. tracheolateralis at A-15.

Heliochera is like *Cotinga*, differing only in that M. sternotrachealis inserts on A-15 and A-16.

Phibalura and *Calyptura* are like *Cotinga*, to judge from Müller's brief descriptions. He mentioned only that they have thin lateral Mm. tracheolaterales and no intrinsic muscles.

Rupicola is like *Cotinga*, differing only in that M. tracheolateralis is broad anteriorly, narrowing at the level of A-15 through A-20, and that M. sternotrachealis is continuous with the dorsal fibers of the lateral muscle. Müller described the "thin lateral muscle" as inserting on "the first really small halfring" ["an den ersten schon schmalen Halbring," (Müller, 1847, p. 31) translated by Bell (Müller, 1878, p. 26) as "the first halfring, which is quite small"]. It is evident from his illustration that Müller did not mean "the first halfring," for he clearly showed the insertion on B-1, with A-1 divided.

Querula is like *Cotinga,* differing as follows. M. tracheolateralis inserts on A-1. M. sternotrachealis is continuous with the dorsal fibers of M. tracheolateralis, which it meets at A-10.

Carpodectes is like *Cotinga,* differing only in that M. tracheolateralis is proportionately half as wide and inserts on A-1; and M. sternotrachealis inserts directly on the lateral surfaces of A-10 through A-12.

Pyroderus is like *Cotinga,* differing as follows. M. tracheolateralis is attached to the center of B-1 by a broad tendon which is folded over the projecting edge of A-1. M. sternotrachealis meets the trachea at A-17 and inserts by a fan-shaped tendon to A-18 through A-23.

Perissocephalus is like *Cotinga,* differing as follows. M. tracheolateralis is free of the trachea from A-9 to A-2, being straight where the lateral surface of the syrinx is concave. M. sternotrachealis inserts on A-11 through A-14. Müller did not mention the muscles in his description of this genus.

Cephalopterus is like *Cotinga,* differing as follows. M. tracheolateralis inserts on the middle of A-1. M. sternotrachealis is continuous with the superficial ventral fibers of the lateral muscle. Tschudi stated that the lateral muscle in his specimen inserted on the fourth bronchial semiring, which was A-1 only if A-5 was complete.

Gymnoderus is like *Cotinga,* differing as follows. M. tracheolateralis bends ventrad in the region of A-20 and broadens so that each muscle covers about one-sixth of the tracheal circumference at A-13, where both the width of the muscle and the dorsoventral diameter of the trachea are greatest. The muscle then bends dorsad, tapering rapidly, and inserts in a narrow area near the dorsal end of B-1. M. sternotrachealis is extremely narrow (possibly an artifact of the age of the specimen) and is continuous with the dorsal superficial fibers of M. tracheolateralis.

Procnias is unlike all of the above. M. tracheolateralis is thick and narrow, inserting on the lateral surface of A-5. A thick pad of intrinsic muscle covers the syrinx, on all sides, from A-4 to B-2. It originates on A-1 through A-4 and extends posteriad to insert on the A-1/B-1 membrane, B-1, the B-1/B-2 membrane, and B-2. Some fibers extend around the dorsal ends of the elements to the medial surface of the internal tympaniform membranes. By far the largest part of the insertion is on the A-1/B-1 membrane, which is tough and fibrous. M. sternotrachealis inserts on the ventrilateral surface of the intrinsic muscle by a broad fan-shaped tendon. A particularly thick part of this tendon is attached to the posterior surface of the muscle. Müller's detailed descriptions and illustrations of *P. alba* and *P. nudicollis* agree closely with the above.

Attila (Pls. 15 and 16) is unlike all of the above. The Mm. tracheolaterales are broad ventrilateral bands for most of their length, each being about 60 degrees of the tracheal circumference wide. They broaden to touch each other at the ventral midline in the region of their insertion, on the ventral two-thirds of A-6. M. sternotrachealis inserts on the lateral surfaces of A-14 through A-16, adjacent to the dorsal edge of M. tracheolateralis. An intrinsic muscle, for which I tentatively employ the name

M. obliquus ventralis, originates adjacent to the ventral midline of A-4 through A-6 and ventrilaterally along A-6 and A-5. It extends laterad and posteriad to insert on the center of the A-1/B-1 membrane.

Casiornis is like *Attila*, differing as follows. The Mm. tracheolaterales meet ventrally at about A-18 and remain in contact to their insertion, on A-5. M. sternotrachealis inserts on A-9 through A-11. M. obliquus ventralis originates midventrally on A-3 through A-5 and laterally along A-5. Its insertion is mostly on A-1, with a few superficial fibers of the dorsal region attached to the A-1/B-1 membrane.

Laniocera is like *Attila*, differing as follows. The Mm. tracheolaterales meet ventrally high on the trachea and remain in contact to their insertion, on A-3 ventrally and on A-4 laterally. M. sternotrachealis inserts on the membranous sheath covering M. tracheolateralis, with a few dorsal fibers in continuity with the latter muscle. M. obliquus ventralis originates on A-3 ventrally and on A-4 ventrilaterally. At their ventral edges the pair overlap. The right muscle originates along the anterior edge of element A-3 on both sides of the midline and its fibers overlie those of the left muscle, which originates on the posterior edge of the element, also on both sides of the midline. They insert symmetrically on the respective A-1/B-1 membranes.

Iodopleura is like *Attila*, differing as follows. The Mm. tracheolaterales are very thin and completely cover the ventral two-thirds of the trachea, inserting on A-3. M. sternotrachealis inserts on the dorsolateral surfaces of A-5 through A-7, with a few fibers continuous with M. tracheolateralis. The intrinsic muscles, apparently Mm. obliqui ventrales, originate on A-3 adjacent to the insertion of the Mm. tracheolaterales and midventrally on the A-2/A-3 membrane. They insert directly on the dorsal ends of the respective halves of B-1. Müller found no intrinsic muscles in *Iodopleura pipra*.

Rhytipterna is like *Attila*, differing as follows. M. sternotrachealis is wholly continuous with the dorsal fibers of M. tracheolateralis. M. obliquus ventralis originates on the midventral region of A-3 and A-4 and ventrilaterally on A-4; it inserts on the ventral half of A-1.

Lipaugus is unlike all of the above. The Mm. tracheolaterales are wide, covering the ventral half of the trachea down to A-13, where they separate and narrow. Each inserts on the middle third of the respective half of B-1. M. sternotrachealis inserts directly on A-9 through A-15, passing through a slot in M. tracheolateralis. There appear to be intrinsic muscles in my specimen, but damage to the ventral region of the syrinx between A-4 and A-8 precludes accurate determination of the myology of that region. On each side is a band of muscle lying superficial to M. tracheolateralis and apparently originating on A-5 and A-6 just medial to the ventromedial edge of the latter muscle. This superficial layer extends obliquely across the extrinsic muscle to insert on B-1, just lateral to the insertion of M. tracheolateralis. Garrod found no intrinsic muscles in *L. cineraceus*.

Pachyramphus is unlike all of the above. The Mm. tracheolaterales converge at about A-35 and their combined mass becomes narrower and thicker toward the insertion. They terminate at A-3 on a single tendinous sheet which shortly divides into two narrow tendons. These are attached to the right and left ventral ends of A-1 and B-1. M. sternotrachealis is a robust muscle which inserts on the ventrilateral surfaces of A-7 through A-11. The exact area of insertion varies slightly among the five specimens. In YPM 1041 (*P. polychropterus*) it is on A-8 through A-10, in YPM 2577 (*P. viridis*) on A-9 through A-11. M. obliquus ventralis originates ventrilaterally on A-3 and A-4, adjacent to M. tracheolateralis, and extends laterally and posteriorly to insert by a broad tendon to the middle of B-1.

In *P. rufus* Müller noted the ventral narrowing of the Mm. tracheolaterales but stated that they terminate at the end of the trachea (A-2); apparently he did not find a tendinous insertion. His description of the intrinsic muscle agrees generally with my findings.

Platypsaris is like *Pachyramphus*, differing as follows. M. tracheolateralis, although similar in shape to that of *Pachyramphus,* lacks the tendinous insertion; it inserts directly on the ventral end of A-1. M. sternotrachealis inserts on A-14 through A-17, with some fibers continuous with the dorsal fibers of M. tracheolateralis. The origin of M. obliquus ventralis includes A-2, as well as A-3 and A-4, and the insertion is atendinous, on the dorsal end of B-1.

In Garrod's description of *P. aglaiae* the positions of the individual muscles are difficult to ascertain. He mentioned that the "syringeal muscles" did not reach the second bronchial semiring (B-1) but he appears to have meant M. tracheolateralis. He stated that this species is identical to *Pachyramphus rufus* as described by Müller, but the illustration of *Platypsaris* shows no oblique intrinsic muscle as shown by Müller. In view of the wide disparity of both descriptions and illustrations it is odd that Garrod should have stressed the similarity of the two syringes.

FAMILY PIPRIDAE. MANAKINS.

Specimens Examined.

Of 56 species in 21 genera, I have examined the following 15 individuals of 11 species and seven genera:

Piprites chloris (Temminck)
Pipra mentalis Sclater, two specimens
Pipra erythrocephala (Linnaeus)
Chiroxiphia lanceolata (Wagler)
Chiroxiphia caudata (Shaw and Nodder), two specimens
Ilicura militaris Parzudaki
Corapipo leucorrhoa (Sclater)
Manacus vitellinus (Gould)
Manacus candei (Parzudaki)
Schiffornis virescens (Lafresnaye)
Schiffornis turdinus (Wied), three specimens

I know of the following descriptions by previous authors:

Pipra erythrocephala (Linnaeus) — Müller (1847, p. 30; Pl. 4, figs. 4, 5; 1878, p. 25)
Pipra pipra (Linnaeus) — Müller (1847, p. 29; Pl. 4, figs. 9-11; 1878, p. 24)
Chiroxiphia pareola (Linnaeus) — Müller (1847, p. 29; Pl. 4, figs. 6-8; 1878, p. 24)
Chiroxiphia pareola (Linnaeus) — Lowe (1942)
Manacus manacus (Linnaeus) — Müller (1847, p. 30; 1878, p. 25)
Manacus vitellinus (Gould) — Lowe (1942)
Schiffornis turdinus (Wied) — Garrod (1877b)

Cartilaginous Elements.

In *Piprites* A-1 through A-3 are divided; A-4 is incomplete dorsally, A-5 and subsequent elements are complete. The pessulus is narrow at its ventral end, where it is fused to A-4, and broad dorsally, where it is fused to A-3L and A-4R. The region between the pessulus and the dorsal ends of A-1, A-2, and A-3R is not membranous, but consists of a thin sheet of soft cartilage. Posteriorly the sheet is about twice as thick as the A-elements and has two short, pointed extensions, directed posteriad. There are no internal cartilages. The B-elements are all divided, B-1 being broad and spatulate at its dorsal end, the others being uniformly narrow.

Schiffornis is unlike *Piprites*. In *S. turdinus* A-1 and A-2 are divided; A-3 and subsequent elements are complete. The pessulus is fused to A-3 at both ends. B-1 is heavier than either the A-elements or the other B-elements and is nearly straight. The result of this straightness is a constriction of the air passages at B-1. A single pair of internal cartilages is attached to the dorsal ends of A-2. They are J-shaped with the curvature directed ventrad. *S. virescens* differs from *S. turdinus* only in that A-3 is incomplete dorsally and is fused to A-4 for its ventral half and at its dorsal end. The pessulus is fused dorsally to A-4. Garrod's description of *S. turdinus* agrees with the above in all major points.

Manacus is unlike both of the above. A-1 through A-4 are divided; A-5 and subsequent elements are complete. A-1 is about twice the width of the other A-elements and has a projection along its posterior edge, to which *M. tracheolateralis* is attached. A-2 is wholly fused to A-1 and to A-3 for its ventral half. The narrow pessulus is fused to the ventral ends of A-2, but is free dorsally. The dorsomedial region between the ends of A-2 and A-3 consists of a sheet of soft cartilage, thickened at its posterior edge. Müller's brief description of *M. manacus* was largely concerned with musculature, but he did state that the "third bronchial ring" (apparently A-1) was very strong. Lowe's remarks on *M. vitellinus* are in accord with the above.

Pipra is unlike all of the above. In *P. erythrocephala* A-1 is divided; A-2, A-3 and A-4 are double; A-5 is incomplete ventrally; A-6 and subsequent elements are complete. A-1 and A-2 are completely fused, as are A-5, A-6 and A-7, the last three forming a rigid drum. The B-elements are soft and quite delicate. B-1 and B-2 are fused into a single broad plate at their dorsal ends. There are no internal cartilages. The pessulus is a medial extension of the dorsal edge of A-5 and is in contact with A-4 for most of its length. It terminates ventrally in an oblong shield that overlies the midventral regions of A-2 through A-5. *P. pipra* differs only in that the drum is composed of A-5 and A-6.

Müller's description and illustration of *P. pipra* differs from the above only in minor points: in his specimen A-2 was divided and there apparently was no drum. In *P. erythrocephala* he found the cartilages to be like those of *P. pipra*.

Corapipo (Pls. 15 and 16) is unlike all of the above. A-1 through A-4 are divided; A-5 through A-7 are incomplete dorsally; A-8 and subsequent elements are complete. The narrow pessulus is fused to A-8 dorsally and to A-5 ventrally. The dorsal ends of A-1 through A-4 are connected by a pair of narrow bars of soft cartilage. There are no internal cartilages. There is a prominent projecting shelf in the middle of B-1 but no muscles are attached to it. The dorsal ends of B-1 and B-2 are spatulate and fused to each other.

Chiroxiphia (Pls. 15 and 16) is unlike all of the above. In *C. lanceolata* A-1 through A-3 are divided; A-4 and A-5 are incomplete dorsally; A-6 and subsequent elements are complete. A-6 through A-11 are fused into a drum, smooth dorsally but showing the fusion seams ventrally. A short mid-dorsal extension of A-6 lies in the dorsal openings of A-4 and A-5. The dorsomedial region from B-1 to A-4 consists of a single sheet of soft cartilage, attached to the dorsal ends of A-1 through A-4 and to the ventral ends of B-1 and A-1. The pessulus and internal cartilages are lacking. *C. caudata* differs from *C. lanceolata* in that A-6 and A-7 are incomplete dorsally and the drum consists of A-8 through A-14. In YPM 2587, A-7R is fused dorsally to the drum and in the AMNH specimen A-7L is fused dorsally to the drum.

Müller's description and illustration of *C. pareola* are similar to the above. He found A-1 through A-3 divided; A-4 through A-6 or A-7 incomplete dorsally; A-8 and subsequent elements complete. In the illustration about seven elements are shown as incomplete dorsally. No mention is made of a drum, and in the illustration only A-11 and A-12 are shown as fused.

Ilicura is unlike all of the above. A-1 through A-5 are divided; A-6 is incomplete dorsally; A-7 and subsequent A-elements are complete. The ventral ends of the divided elements are narrow and slightly spatulate. The dorsal ends of B-1 and A-1 through A-5 are connected by a bar of soft cartilage. The pessulus extends from A-2 ventrally to A-6 dorsally and is free at both ends. The difference between A-1 and B-1 is not as great as in most manakins, B-1 being close to and parallel to A-1, but different in consistency and cross section. The ventral ends of B-1 are almost completely fused. The bronchi are short and strongly tapered, there being only seven B-elements.

Musculature.

In *Piprites* the Mm. tracheolaterales are narrow lateral bands inserting directly on the center fifth of B-1. M. sternotrachealis is wholly continuous with the dorsal half of M. tracheolateralis, which it meets at the level of A-8. There are no intrinsic muscles.

Schiffornis is unlike *Piprites*. M. tracheolateralis is of medium width, occupying the lateral 60° of the trachea on each side. It inserts on A-4 through A-6 in *S. turdinus* and on A-3 through A-5 in *S. virescens*. M. sternotrachealis inserts directly on A-9 and A-10, dorsally adjacent to M. tracheolateralis. A short, broad intrinsic muscle originates immediately posterior to the insertion of M. tracheolaterales and extends posterodorsad to insert by a short tendon to the subterminal dorsal quarter of B-1. In one specimen of *S. turdinus* the intrinsic muscle is covered by a thin, but full-width extension of M. tracheolateralis, which inserts just beyond the intrinsic muscle.

In his description of *S. turdinus* Garrod mentioned only M. tracheolateralis, which he found to insert in the center of "the second bronchial semiring" (A-1). Apparently he did not find an intrinsic muscle.

Manacus is unlike all of the above. The Mm. tracheolaterales converge at the level of A-27 and thicken midventrally, resulting in a prominent bulge in the region of A-4 through A-7. The majority of the thick portion consists of the left muscle, the fibers of which lie down on both sides of the ventral midline, but insert only on the left. The insertion is along the ventral seven-eighths of A-1. M. sternotrachealis is continuous with the lateral superficial fibers of M. tracheolateralis, which it meets at

A-11. There is no intrinsic muscle. Müller's description of *M. manacus* and Lowe's of *M. vitellinus* agrees closely with the above description, which is based on *M. candei* and *M. vitellinus*. Lowe illustrated but did not describe a peculiar form of M. sternotrachealis in which the pair of muscles share a midventral tendon with diffuse attachment. I have not found such a condition.

Pipra is unlike all of the above. M. tracheolateralis inserts ventrally and ventrilaterally on the anterior edge of the drum; i.e. on A-6 in *P. mentalis* and A-7 in *P. erythrocephala*. M. sternotrachealis inserts on the membranous sheath surrounding M. tracheolateralis. The intrinsic muscle originates broadly near the anterior edge of the drum, immediately posterior to the insertion of M. tracheolateralis. It extends posteriad to insert directly on nearly the entire surface of A-1. In *P. pipra* Müller found no intrinsic muscle. Instead, he described M. tracheolateralis as divided into two fasciculi, which inserted on separate areas of A-1.

Chiroxiphia (Pls. 15 and 16) is unlike all of the above. The Mm. tracheolaterales cover the ventral half of the trachea for most of their length, inserting on the anterior edge of the drum, A-11 in *C. lanceolata* and A-14 in *C. caudata*. M. sternotrachealis is wholly continuous with the superficial lateral fibers of M. tracheolateralis. A broad, thick intrinsic muscle originates on the anterior edge of the drum from the ventral midline to the dorsolateral surface. Müller stated that the muscle consisted of three longitudinal portions, but no such divisions exist in my specimens. The majority of the muscle's mass is in the dorsolateral region. The insertion has three components. In *C. lanceolata* the muscle inserts ventrally by a broad tendon to A-2 and dorsolaterally by two narrow tendons, to the dorsal ends of A-1 and B-1, respectively. *C. caudata* differs only in that the broad ventral tendon is attached to A-1.

Ilicura is unlike all of the above. The Mm. tracheolaterales converge at about A-25 and cover the ventral two-thirds of the trachea to their insertion on A-4 and A-5 ventrally, on A-6 ventrilaterally and, with a dorsolateral extension, on the dorsal end of B-1. The torsion of this muscle is such that fibers from the left muscle insert about 30° to the right of the ventral midline. The Mm. sternotracheales insert on the membranous sheath surrounding the Mm. tracheolaterales, with a few fibers attached directly to A-15 and A-16 at the dorsal edge of the latter muscle.

There is a single pair of intrinsic muscles, which I tentatively call Mm. obliqui ventrales, due to their similarity to those muscles in the Tyrannidae. Each of the pair originates adjacent to the ventral midline of A-2 and A-3 and also ventrally and ventrilaterally on A-4 and A-5. It extends posterolaterally and posterodorsally to insert along nearly the entire length of B-1. At its dorsal edge this muscle is in contact with the extension of M. tracheolateralis.

Corapipo (Pls. 15 and 16) is unlike all of the above. The Mm. tracheolaterales cover the ventral half of the trachea from about A-38 to A-8, where they diverge ventrally and bend dorsad, inserting along a line from the ventrilateral surface of A-7 to the lateral surface of A-4. Approximately the dorsal sixth of the fibers extend to A-1. M. sternotrachealis is extremely robust and inserts directly on the lateral surface of A-15 through A-26, adjacent to the dorsal edge of M. tracheolateralis.

There are two pairs of intrinsic muscles. The ventral one originates immediately posterior to the insertion of M. tracheolateralis, from A-7 to A-4 and on the lateral surfaces of A-3 and A-2. It extends posteroventrad to insert on the ventral end of A-1, wrapping itself around the end of the element. The dorsal muscle originates on the lateral surface of A-2 and A-3 and extends posterodorsad to insert on the dorsal end of A-1, just lateral to the insertion of the extension of M. tracheolateralis.

FAMILY TYRANNIDAE. TYRANT FLYCATCHERS.

SUBFAMILY FLUVICOLINAE.

Specimens Examined.

Of the 70 species in 27 genera, I have examined the following 46 individuals in 28 species and 21 genera:

Agriornis livida (Kittlitz)
Agriornis microptera Gould
Xolmis coronata (Vieillot)
Xolmis irupero (Vieillot)
Xolmis pyrope (Kittlitz), two specimens
Muscisaxicola albilora Lafresnaye
Muscisaxicola maculirostris Lafr. and D'Orb.
Lessonia rufa (Gmelin)
Neoxolmis rufiventris (Vieillot), two specimens
Ochthoeca fumicolor Sclater, two specimens
Sayornis phoebe (Latham), three specimens
Sayornis nigricans (Swainson)
Sayornis saya (Bonaparte)
Colonia colonus (Vieillot), three specimens
Gubernetes yetapa (Vieillot), two specimens
Yetapa risora (Vieillot)
Knipolegus nigerrimus (Vieillot)
Knipolegus cyanirostris (Vieillot), three specimens
Phaeotriccus hudsoni (Sclater)
Entotriccus striaticeps (Lafr. and D'Orb.)
Lichenops [= Hymenops] perspicillata (Gmelin)
Muscipipra vetula (Lichtenstein)
Fluvicola climazura (Vieillot)
Arundinicola leucocephala (Linnaeus)
Pyrocephalus rubinus (Boddaert), five specimens
Muscigralla brevicauda (Lafr. and D'Orb.) two specimens
Satrapa icterophrys (Vieillot), two specimens
Machetornis rixosa (Vieillot), three specimens

I know of only the following descriptions by previous authors:

Lessonia rufa (Gmelin) — Müller (1847, p. 35; Pl. 6, fig. 7; 1878, p. 29)
Sayornis phoebe (Latham) — MacGillivray (1839)
Sayornis phoebe (Latham) — Miskimen (1963)
Fluvicola pica (Boddaert) — Müller (1847, p. 35; Pl. 6, figs. 8, 9; 1878, p. 29)
Pyrocephalus rubinus (Boddaert) — Müller (1847, p. 34; Pl. 5, figs. 6. 7; 1878, p. 28)
Machetornis rixosa (Vieillot) — Müller (1847, p. 34; 1878, p. 28)

Cartilaginous Elements.

In *Xolmis* (Pls. 5 and 6), A-1 through A-4 are divided; A-5 and other A-elements are complete. A-2, A-3 and A-4 are weakly fused at their dorsal ends to a triangular plug of soft cartilage which fills the dorsomedial region adjacent to these elements and extends ventrad to connect the ventral ends of the same elements. All of the B-elements are divided. The internal cartilages are rounded triangles, with their pointed ends posteriad and their anterior edges weakly fused to the cartilaginous plug. There is no pessulus, but in the following genera compared with *Xolmis* the pessulus is present unless otherwise noted.

Phaeotriccus is like *Xolmis*, differing as follows. A-3 is double, with the medial section white, spongy cartilage. A-4 is complete and indented mid-dorsally. The pessulus is fused to A-4 at both ends and is completely hidden by the cartilaginous plug.

Pyrocephalus is like *Xolmis*, differing only in that the fusion of the internal cartilages to the plug is more complete. Müller (1847, p. 35) reported the "first bronchial ring," apparently A-2, to be double ("vollstandig") and A-3 complete. In one of my specimens (YPM 2766) A-4 is slightly longer medially than in the other specimens, approaching the double condition. Considering the relative uniformity among my five specimens, Müller's must be considered an extreme variant.

Knipolegus is like *Xolmis*, differing only in that the internal cartilages are completely fused to the cartilaginous plug, with no joint visible.

Neoxolmis is like *Xolmis*, differing as follows. A-5 is divided. In YPM 2736, A-5R is fused dorsally to A-6. The internal cartilages are broader than those of *Xolmis* and slightly crescent-shaped.

Gubernetes is like *Xolmis*, differing as follows. Only A-1, A-2 and A-3 are divided; A-4 is complete and is fused to the cartilaginous plug at the dorsal midline. The internal cartilages are J-shaped, with the curve directed posteriad and ventrad.

Agriornis is like *Xolmis*, differing as follows. In the specimen of *A. livida* there is a supernumerary component, A-4aR, the dorsal end of which does not reach the cartilaginous plug. At its ventral end A-4aR tapers to about one half its usual width and lies very close to A-5. There are two pairs of internal cartilages: one pair completely fused to the cartilaginous plug, consisting of straight bars, and a second pair, posterior to the ends of the first, consisting of short bars oriented at right angles to the first pair.

Fluvicola is like *Xolmis*, but my specimen is too damaged by shot to make detailed analysis possible. All of the A-elements appear to be like those of *Xolmis*.

Muscisaxicola is like *Xolmis*, differing only in that A-5 is divided and fused to the cartilaginous plug, as are A-2 through A-4.

Satrapa and *Entotriccus* are like *Xolmis*, differing as follows. A-4 is not fused to the cartilaginous plug. The proportions of all of the elements are much more delicate than those of *Xolmis;* the membranous interspaces are proportionately wider. The internal cartilages are J-shaped and fused to the cartilaginous plug anteriorly.

Muscipipra appears to be like *Xolmis*, but in my specimen the entire ventral portion of the syrinx was removed by shot, as well as most of the right bronchus and part of the mid-dorsal region. From the remainder the following points can be made out. A-1 through A-3 are divided; A-4 is complete and is fused to the cartilaginous plug. A-2 is not fused to the plug.

Yetapa is like *Xolmis*, differing as follows. A-1 through A-4 are fused dorsally to the cartilaginous plug. These four elements are joined at their ventral ends by a band of soft cartilages. B-1 is strongly curved inward at both ends.

Lichenops (Pls. 7 and 8) is strikingly different from *Xolmis*. A-1, A-2 and A-3 are divided; A-4 and A-5 are incomplete dorsally and are joined at their dorsal ends. All except A-1 are fused dorsally to the cartilaginous plug. The latter has prominent ridges in line with the attached elements. The ventral ends of A-1, A-2, and A-3 are joined by an inverted "U" of soft cartilage, which has an anterior extension lying superficial to the midventral regions of A-4 through A-7 and joined to them. Lying in the midsagittal plane and fused to this "U" is a hook of stiff cartilage directed anteriad.

Colonia (Pls. 5 and 6) is also different from all of the above. A-1, A-2 and A-3 are divided and the remaining A-elements are complete. The concavity of A-1 and A-2 is directed nearly posteriad and at the lateral edge of A-1 is a projecting shelf occupying the middle quarter of the element. In the YPM specimen and the second AMNH specimen A-2 is fused to A-3 at the dorsal end. In the first AMNH specimen the dorsal cartilages are asymmetrical; A-2L and A-3L are fused but A-2R is discrete, while A-3R is fused to A-4. The cartilaginous plug is small and is attached to the dorsal ends of A-2 and A-3 only. It has a medial extension reaching ventrad about two-thirds of the distance to the ventral ends of A-2. The internal cartilages are rounded triangles, flexibly joined to the cartilaginous plug.

Ochthoeca is like the YPM specimen of *Colonia*, differing only in that A-1 lacks the projecting shell.

Muscigralla is like *Colonia*, differing as follows. A-1 and A-2 are divided; A-3 is complete. There is no fusion of elements. The small cartilaginous plug is fused to the dorsal ends of A-2 and to the mid-dorsal posterior edge of A-3. The internal cartilages are long narrow bars fused to the plug and extending posteriad to the level of B-2.

Arundinicola is like *Colonia*, differing as follows. A-3L is fused to a short mid-dorsal posteriad extension of A-4, while A-3R is free. A narrow extra component, A-3aR, located very close to A-4, is also fused dorsally to the same extension. There is a short free pessulus. There are two pairs of internal cartilages: a long dorsal pair lightly attached to the pessulus and extending posteriad to the level of B-2; and a small circular ventral pair fused to the ventral end of the pessulus.

Sayornis also differs markedly from all of the above. None of my specimens shows any fusion of elements. In *S. nigricans* A-1, A-2 and A-3 are divided. A-4 is complete and has a mid-dorsal posteriad extension which curves ventrad, forming the pessulus, free at the ventral end. The pessulus is partially covered by a small cartilaginous plug, attached to the dorsal ends of A-2 and A-3. The internal cartilages are rounded equilateral triangles fused flexibly to the plug. In *S. phoebe* A-1 through A-4 are divided and the pessulus is an extension of A-5. The cartilaginous plug is a transverse bar connecting the dorsal ends of A-2, A-3 and A-4. The internal cartilages are short straight bars fused to the cartilaginous plug and extending posteriad to the level of A-1. *S. saya* differs from *S. phoebe* only in that A-5 and A-6 are incomplete dorsally.

In MacGillivray's description of the syrinx in *S. phoebe* A-1 and A-2 are divided ("dimidiate") and A-3 complete. Miskimen's specimens of *S. phoebe* fit the above description except that A-4, A-5 and A-6 are fused ventrally.

Lessonia (Pls. 5 and 6) is unlike all of the above. A-1 through A-4 are divided; A-5 and A-6 are incomplete dorsally. A-7 is complete and has a long mid-dorsal extension lying between the dorsal ends of A-6, A-5, and A-4. The edges of the extension are indented to accept the ends of the elements, which are not fused to it. There is no cartilaginous plug and no pessulus. The internal cartilages are shield-shaped, with their broad ends anteriorly, and close to but not fused to the dorsal ends of A-2.

Machetornis (Pls. 7 and 8) is strongly different from all of the above. A-1 is divided and A-2 double; A-3 and other A-elements are complete. A-3 has a mid-dorsal posteriad extension which tapers into an extremely thin pessulus, free at its ventral end. There is no cartilaginous plug. The internal cartilages are small and elliptical and are not fused to any other elements. B-1 consists of a pair of nearly straight bars lying very close to A-1. B-2, whose ends touch those of B-1, consists of a pair of near-semicircles, half as thick as B-1. The bronchi of *Machetornis* are considerably longer and less tapering than those of the above genera.

Musculature.

In *Xolmis pyrope* and *X. irupero*, M. tracheolateralis covers the ventral half of the trachea posterior to A-30. It inserts directly on A-5, ventrally and laterally, mostly near the anterior edge of the element. M. sternotrachealis originates on the interior surface of the coracoid process of the sternum. Near its insertion on the trachea it fans out into a broad flat sheet which inserts on the tough membrane overlying M. tracheolateralis. A few of the dorsal fibers insert directly on the lateral surfaces of A-15 through A-19. M. obliquus ventralis originates along the ventral midline on A-3, A-4 and A-5 as well as ventrilaterally on A-5. The dorsal limit of its origin is in line with the dorsal edge of M. tracheolateralis. The insertion of M. obliquus ventralis covers the center third of A-1. *X. coronata* is identical to the other two, except that the lateral origin of M. obliquus ventralis is on A-4, resulting in a shorter lateral portion of the muscle.

Neoxolmis is like *Xolmis*, differing as follows. M. tracheolateralis inserts along a line extending from A-4 ventrally to A-2 laterally. M. obliquus ventralis originates midventrally on A-2, A-3, and A-4 and posterior to the insertion of M. tracheolateralis. Its insertion is along the ventral two-thirds of A-1, except for a small part of the ventral end. The two specimens differ in the region of insertion of M. sternotrachealis, but in both the mode of insertion is as in *Xolmis*. In YPM 2739 the insertion is at the level of A-13 through A-23; in YPM 2736 it is at A-26 through A-33.

Entotriccus is like *Xolmis*, differing as follows. The dorsal third of M. sternotrachealis, instead of inserting directly, is continuous with the superficial fibers of M. tracheolateralis. The superficial fibers of M. obliquus ventralis originate midventrally on A-3, A-4 and A-5 and only slightly off the ventral midline on A-5. The deeper fibers attach to A-4 from the ventral midline about halfway to the dorsal midline. A few of the fibers at the dorsal edge of the muscle originate on A-3. The insertion is on the center third of A-1, as in *Xolmis*.

Gubernetes is like *Xolmis*, differing as follows. M. tracheolateralis inserts along the anterior edge of the ventral two-thirds of A-3. M. sternotrachealis has two fasciculi, a ventral one which inserts on the membrane covering M. tracheolateralis, and a dorsal one, about one-third of the muscle, inserting on A-10, A-11, and A-12 adjacent to the dorsal edge of M. tracheolateralis. M. obliquus ventralis originates on the edge of A-3, posterior to the insertion of M. tracheolateralis, and inserts on the center third of A-1.

Muscipipra appears to be like *Xolmis,* but shot damage prevents positive comparisons of the ventral muscles. M. tracheolateralis covers the ventral half of the trachea from A-28 to its insertion on A-3 laterally and probably on A-4 ventrally. M. sternotrachealis has two fasciculi: the dorsal one inserting directly on A-14 through A-19 and the ventral one continuous with M. tracheolateralis. The lateral fibers of M. obliquus ventralis originate on A-3 and insert on A-1.

Fluvicola is like *Xolmis,* differing as follows. M. tracheolateralis inserts on A-4 ventrally and on A-3 laterally. M. sternotrachealis is proportionately heavier than in *Xolmis* and has only slight continuity with M. tracheolateralis, the majority of the fibers inserting on the membranous sheath surrounding the latter muscle. The ventral fibers insert on a median raphe which is continuous with the sheath. M. obliquus ventralis originates on A-3 and A-4 ventrally and on A-3 laterally, inserting as in *Xolmis.*

Satrapa is like *Xolmis,* differing as follows. In addition to its ventral insertion on A-5, M. tracheolateralis sends a lateral extension to insert on A-2 beneath M. obliquus ventralis. M. sternotrachealis is very thin and inserts directly on A-16 through A-21, adjacent to the dorsal edge of M. tracheolateralis.

Agriornis is like *Xolmis,* differing as follows. M. tracheolateralis inserts on A-5 and is very thick ventrally. M. sternotrachealis is thin (about one-sixth the diameter of the trachea) and inserts adjacent to the dorsal edge of M. tracheolateralis on A-12 through A-14 in *A. livida* and on A-10 through A-13 in *A. microptera.* In both specimens M. obliquus ventralis originates on A-5 ventrally and A-4 laterally as well as on the A-4/A-5 membrane. It inserts on A-1. The muscle has distinct ventral and lateral parts, but both the origin and insertion are continuous from one edge of the muscle to the other.

Lessonia (Pls. 5 and 6) is unlike all of the above. M. tracheolateralis covers the ventral half of the trachea posterior to A-38, inserting on A-3 ventrally and on A-4 laterally. M. sternotrachealis is very thick (about half the diameter of the trachea). Its insertion is slightly asymmetrical: the posterior edge of the right muscle is at A-5, that of the left at A-6. The posterior half of each muscle inserts on the membranous sheath surrounding the Mm. tracheolaterales. The two Mm. sternotracheales interdigitate ventrally from A-6 to about A-12. The anterior fibers are continuous with the lateral superficial ones of Mm. tracheolaterales. M. obliquus ventralis is small, originating on A-3 and extending parallel to the bronchial axis to its insertion on the ventral quarter of A-1. Müller's description of *Lessonia* stated only that the tracheal and syringeal muscles are like those of *Fluvicola bicolor.*

Phaeotriccus is like *Lessonia,* differing as follows. About one-tenth of the fibers of M. sternotrachealis, at the posterior edge of the muscle, are continuous from one member of the pair to the other. M. obliquus ventralis originates on a median raphe attached midventrally to A-2 and A-3.

Muscisaxicola is like *Lessonia,* differing as follows. The Mm. sternotracheales are symmetrical and their insertion on the sheath extends from A-8 to A-15, beyond which the fibers are continuous with the Mm. tracheolaterales. A narrow extension of M. tracheolateralis near the dorsal edge reaches A-1 adjacent to M. obliquus ventralis. The latter originates directly on A-3 midventrally and on A-4 ventrally and laterally; the insertion is on A-1.

Knipolegus is like *Lessonia,* differing as follows. M. sternotrachealis inserts more anteriorly, at the level of A-12 through A-18. The posterior tenth of the fibers are continuous from one of the pair to the other. A few of the dorsal fibers insert directly on A-11 through A-14 at the dorsal edge of M. tracheolateralis. The M. obliquus ventralis originates near the ventral midline on A-2 through A-5, directly. It extends posterolaterally to insert broadly in the center of A-1.

Lichenops (Pls. 7 and 8) differs markedly from all of the above. M. tracheolateralis covers the ventral half of the trachea from A-46 to its insertion on A-6. M. sternotrachealis is very thick, its longer diameter being about one-third that of the trachea. Its insertion is almost entirely on the membranous sheath around M. tracheolateralis, a few of the dorsal fibers inserting directly on the lateral surfaces of A-13 through A-16. The origin of M. obliquus ventralis covers a large area, ventrally on the cartilaginous hook and on the tough vane enclosed by it; laterally and dorsolaterally on A-5 and A-6. The direction of the superficial fibers is nearly anteroposterior; the deep fibers run almost at right angles to them, the transition being gradual. The insertion covers nearly the entire length of A-1 and a small portion of the ventral end of the A-1/B-1 membrane. The belly of the muscle bulges so strongly that it covers the insertion of M. tracheolateralis.

Sayornis (Pls. 5 and 6) also differs widely from all of the above. In all three species, M. tracheolateralis covers the ventral half of the trachea from the convergence of the pair in the low A-30's (variable) to its insertion ventrally on A-2 and laterally on the anterior edge of A-1. In *S. phoebe* and *S. saya* the insertion of M. sternotrachealis is directly on approximately A-10 through A-13 (variable) at the dorsal edge of M. tracheolateralis. In *S. nigricans*, M. sternotrachealis reaches M. tracheolateralis at the level of A-10 and A-11, passes through the latter muscle in small fasciculi and inserts directly on A-10 and A-11 beneath M. tracheolateralis. In *S. nigricans* and *S. phoebe*, M. obliquus ventralis has two layers. The superficial one is a continuous band of fibers extending from the ventral half of A-1L to the corresponding portion of A-1R. In a sense, this band, being symmetrical, has two insertions and no origin. The deep layer originates near the ventral midline on A-2 through A-5, both directly and by a short raphe. It extends posterolaterally to insert on A-1 just anterior to the insertion of the superficial layer. *S. saya* lacks the superficial layer but is otherwise similar to the other members of the genus.

Miskimen (1963) gave quite a different description of the syrinx of *S. phoebe*. In her two specimens she found M. tracheolateralis inserting on A-8. M. obliquus ventralis apparently originated in the same manner and location as the deeper layer of my specimens, but the superficial layer was lacking, as in *S. saya*. Moreover, she found the muscle inserting on the dorsal ends of A-1, A-2 and A-3.

Arundinicola is like *Sayornis*, differing as follows. M. tracheolateralis inserts ventrally on A-4, ventrilaterally on A-5, and laterally on A-4. M. sternotrachealis inserts directly at the dorsal edge of M. tracheolateralis on the lateral surface of A-10 through A-13. M. obliquus ventralis originates midventrally on A-2 and A-3 and inserts in the center of the A-1/B-1 membrane. The anterior third of the fibers are continuous from one side to the other, superficial to the insertion of M. tracheolateralis.

Muscigralla is like *Sayornis*, differing as follows. M. tracheolateralis inserts ventrilaterally and laterally on A-2. M. sternotrachealis inserts partly on the ventral part of the sheath around M. tracheolateralis and partly as in *Sayornis*, on A-11, A-12 and

A-13. M. obliquus ventralis originates on a median raphe attached to the ventral ends of A-2 through A-4, and extends, superficial to the insertion of M. tracheolateralis, to insert on the ventral half of A-1.

Pyrocephalus (Pls. 7 and 8) is very different from all of the above genera. M. tracheolateralis covers the ventral half of the syrinx posterior to about A-28 (variable). The lateral fibers insert on A-4, while the main part of the muscle tapers almost to a point midventrally, inserting on A-2 and A-3 near the ventral midline. M. obliquus ventralis originates on the ventral region of A-2 and A-3 adjacent to the point of M. tracheolateralis and inserts near the center of the A-1/B-1 membrane. Although a narrow muscle, compared with that of many tyrannids, it is variable. In YPM 2177 M. obliquus ventralis is only about one-third the width of M. tracheolateralis; in YPM 2768 the former is nearly as wide as the latter; the other three specimens are intermediate. Müller's description and illustration of the syrinx of *Pyrocephalus* closely approximates that of my specimen YPM 2177.

Yetapa is like *Pyrocephalus,* but the specimen at hand appears to have been dried in preparation, making accurate comparison difficult. The following differences are apparent. M. sternotrachealis inserts wholly on the lateral surfaces of A-19 through A-26. M. obliquus ventralis originates along the ventral half of A-3 and inserts on the A-1/B-1 membrane. It is broader than in any of the specimens of *Pyrocephalus*, being the full width of M. tracheolateralis.

Colonia (Pls. 5 and 6) differs markedly from all of the above. M. tracheolateralis covers the ventral two-thirds of the trachea from about A-31 to its insertion on A-3 ventrally and A-4 laterally. M. sternotrachealis is wholly continuous with the superficial fibers of M. tracheolateralis, which it meets at the level of A-16. M. obliquus ventralis originates on A-2 near the ventral midline, on the connective tissue between A-2 and A-3, and laterally along A-3 about two-thirds of the distance to the dorsal midline. In the first and third specimens listed the fibers are strongly bunched at the dorsal and ventral edges of the muscle, leaving it thin in the middle. In the second specimen, the muscle is of uniform thickness. In all three the origin is continuous over its entire width. The insertion is on the projecting shelf in the center of A-1.

Ochthoeca is unlike all of the above. M. tracheolateralis consists of a narrow lateral strip, broadening near its insertion, on the lateral two-thirds of A-4 and dorsolaterally on A-5. The members of the pair meet ventrally at A-6. M. sternotrachealis inserts directly on A-14 through A-18, at the dorsal edge of M. tracheolateralis. M. obliquus ventralis originates on the ventral half of A-4 with some of the deep fibers attached to A-3. It inserts along the ventral half of A-1, except for the extreme ventral end. M. obliquus dorsalis (see Pl. 1, fig. 6,) originates by a short raphe on the dorsal midline of A-4 and A-5. It extends posterolaterally to insert directly on a small area of A-1 adjacent to the insertion of M. obliquus ventralis.

Machetornis (Pls. 7 and 8) is unlike all of the above. M. tracheolateralis covers the ventral half of the trachea from A-40 (variable) to A-5 (all specimens) where the members of the pair diverge. It inserts directly on the ventral half of A-1. M. sternotrachealis inserts ventrally on the membranous sheath around M. tracheolateralis, laterally in continuity with the superficial fibers of the latter, and dorsally on A-12 through A-17. The direction of M. sternotrachealis is such that it lies against M. tracheolateralis at the level of A-3. There are no intrinsic muscles.

SUBFAMILY TYRANNINAE.

Specimens Examined.

Of 34 species in 13 genera, I have examined the following 29 individuals in 19 species and 12 genera:

Muscivora tyrannus (Linnaeus)
Tyrannus tyrannus (Linnaeus), three specimens
Tyrannus albogularis Burmeister
Tyrannus melancholicus Vieillot
Tyrannus dominicensis (Gmelin)
Empidonomus aurantioatrocristatus (Lafr. and D'Orb.)
Legatus leucophaius (Vieillot)
Sirystes sibilator (Vieillot), two specimens
Myiodynastes luteiventris Sclater, three specimens
Myiodynastes bairdii Gambel
Megarhynchus pitangua (Linnaeus)
Conopias trivirgata (Wied)
Myiozetetes cayanensis (Linnaeus), three specimens
Myiozetetes similis (Spix), three specimens
Myiozetetes granadensis Lawrence
Tyrannopsis sulphurea (Spix)
Pitangus sulphuratus (Linnaeus), two specimens
Pitangus lictor Lichtenstein
Tolmarchus caudifasciatus (D'Orbigny)

I know of only the following descriptions in literature:

Muscivora tyrannus (Linnaeus) — Miskimen (1963)
Tyrannus melancholicus Vieillot — Müller (1847, p. 34; 1878, p. 28)
Tyrannus tyrannus (Linnaeus) — MacGillivray (1839, p. 421)
Tyrannus tyrannus (Linnaeus) — Miskimen (1963)
Pitangus sulphuratus (Linnaeus) — Müller (1847, p. 33; Pl. 3, figs. 1-5; 1878, p. 27)

Cartilaginous Elements.

Tyrannus (Pls. 9 and 10) is typical of a large section of the subfamily. In *T. tyrannus* A-1 is divided. A-2 is double; the medial portion of each component is very straight and meets the lateral portion with a noticeable "corner." The two components are fused at their ventral ends. A-3 and A-4 are variable among my specimens. In YPM 706 A-3 is divided, A-4 incomplete dorsally, and A-5 complete. In YPM J-761 A-4 is complete and in the unnumbered specimen both A-3 and A-4 are complete. In YPM 706 and YPM J-761 the pessulus is a small rigid bar extending from the space between the dorsal ends of A-3, about two-thirds of the distance to the ventral junction of A-2. The pessulus is lacking in the unnumbered specimen. The B-elements are narrow (about half as wide as the A-elements), divided, and lie parallel to A-1. B-1 and B-2 are connected by a short bridge of cartilage at their ventral ends. Each B-element posterior to B-4 has a bony cap covering the middle third of the component.

The internal cartilages are straight bars flexibly attached to the dorsal ends of A-2 and extending posteriad to the level of B-2. YPM 706 will serve as the basis for comparison with other genera.

Tyrannus melancholicus and *T. dominicensis* are like *T. tyrannus* in all respects. *T. albogularis* differs only in that A-4 is divided and A-5 is incomplete ventrally.

Müller stated that in *Tyrannus melancholicus* A-2, A-3, and A-4 are double ("ganze") but gave no other information. In *T. tyrannus,* MacGillivray found A-1 and A-2 divided and the pessulus lacking. Miskimen's description of *T. tyrannus* agrees with that of YPM 706 (above), except that in her specimen A-4 is divided instead of incomplete dorsally. Instead of fusion, elements A-1 through A-4 are joined by connective tissue. The pessulus is lacking.

Muscivora is like *Tyrannus,* differing as follows. A-3, A-4, and A-5 are incomplete ventrally. A-1 through A-4 are fused at their ventral ends and for about one-third of their lengths. There is no pessulus. The internal cartilages are J-shaped with the curved section directed ventrad. They are fused to the dorsal "corners" of A-2.

Miskimen's description of *Muscivora* agrees with the above, except that in her specimen both A-3 and A-4 ("syringeo-bronchial rings") were double and only A-3, A-4, and A-5 ("drum") were fused ventrally. A-5 was complete, and the pessulus was lacking.

Tyrannopsis is like *Tyrannus,* differing only in that the lower A-elements are proportionately narrower and the internal cartilages slightly longer.

Myiodynastes is like *Tyrannus,* differing as follows. The two components of A-2 do not touch. Both A-3 and A-4 are divided. A-5 has a short midventral extension filling the space between the ventral ends of A-4. On YPM 1047 this extension is lacking and in its place is a small bony disc attached to the ventral end of the pessulus. The latter is a cartilaginous bar constituting the ventral half of the junction of the internal tympaniform membranes.

Megarhynchus is like *Tyrannus,* differing as follows. The ventral ends of A-1 and A-2 do not touch their opposite members. The region between the ventral ends of A-3 is membranous, but the internal tympaniform membranes extend to the level of A-4, so that the ventral ends of A-3 have the air sac on both sides of them. The middorsal region differs from that of *Tyrannus* in having a broad plug of cartilage extending from the medial sections of A-2 to the middle of A-4, replacing the pessulus. The ventral ends of B-3 are held in contact by tough connective tissue. The internal cartilages are ⅃-shaped, with the short arm directed ventrad.

Tolmarchus is like *Tyrannus,* differing as follows. The dorsomedial corner of A-2 is rounded. The pessulus is a small plate located between the medial sections of A-2 and fused to them ventrally.

Conopias is like *Tyrannus,* differing as follows. A-4 is complete, as are the anterior A-elements. In the region of B-3 through B-6 the bronchi are so close that the ventral ends of the elements dovetail and are held in that position by tough connective tissue. The internal cartilages are ⅃-shaped.

Empidonomus is like *Tyrannus,* differing as follows. A-1, A-2, and A-3 are about half the width of the other elements and are unfused. A-4 and A-5 are completely fused. The internal cartilages are short, extending only to the level of B-1. There is no pessulus.

Pitangus sulphuratus and *P. lictor* differ considerably from each other. *P. sulphur-*

atus is like *Tyrannus*, differing as follows. A-2 through A-5 are double and are closely fitted together, but not fused. There is no pessulus; its place is occupied by the medial portions of A-4 and A-5. The B-elements are unusually stiff but are divided and shaped as in other genera. B-1 is in contact with A-1 for most of its length. B-2 touches B-1 only at its ends, which are thickened and spatulate. B-3 and B-4 are connected ventrally by a stiff bar forming a "U" and the two "U's" are held together by fibrous connective tissue. Müller's description of *Pitangus* is like the above, except that he neither mentioned nor illustrated the bar connecting B-3 and B-4.

Pitangus lictor is markedly different from *Tyrannus*. A-2 is divided, but nearly double, the medial section extending about three-quarters of the distance from the dorsal to the ventral side. The medial portion is broader than the lateral portion of the element and is made of spongy white cartilage. A-3 is like A-2 except that the medial section is narrow, stiff and transparent. A-4 and A-5 are divided rings of the usual C-shape. A-6 and remaining A-elements are complete. The internal cartilages are short narrow bars attached to the dorsal end of the medial section of A-2. There is no pessulus.

Legatus (Pls. 7 and 8) differs strongly from all of the above. A-1, A-2, and A-3 are divided; A-4 is incomplete ventrally. A-2 and A-3 are fused for their dorsal halves only. A cartilaginous plug fills the mid-dorsal region from A-4 (to which it is fused) about two-thirds of the way to the ventral side of the internal tympaniform membranes. It is fused to the dorsal ends of A-2 and A-3. The pessulus is a median bony plate completely covered by the plug and extending from the region between the dorsal ends of A-3 halfway to the ventral ends of that element. The internal cartilages are J-shaped and are not attached to other elements.

Sirystes differs from all of the above. In YPM 2790, A-1 through A-4 are divided and A-5 and subsequent elements are complete. A-4L is completely fused to A-5. The cartilaginous plug is saddle-shaped, extending dorsally to the ends of A-2, A-3, and A-4 (to which it is fused) and ventrally to about midway between the dorsal and ventral surfaces. There is no pessulus. The internal cartilages are J-shaped, with the curved part directed ventrad. All the B-elements are divided, with slightly spatulate ends. The other specimen, YPM 2791, differs from the first in that A-4 is incomplete ventrally and wholly free from A-5. All of the elements are narrower than those of YPM 2790, with wider membranes between them. The cartilaginous plug is attached to A-2 and A-3 only. The internal cartilages are J-shaped with the short arm directed ventrad.

Myiozetetes is unlike all of the above, and the seven specimens vary among themselves. Because of its symmetry YPM 1543 (*M. similis*) will be described as "typical" (Pls. 9 and 10). A-1 is divided; A-2 is double, the two medial sections being fused at their ventral ends; A-3, A-4, and A-5 are divided; A-6 and A-7 are complete and are fused over their entire length; A-8 is complete and unmodified. The pessulus is a stiff, narrow plate extending from the region between the dorsal ends of A-5 to the ventral ends of A-2, which it touches. The internal cartilages are straight, are attached to the dorsomedial region of A-2, and extend to the level of B-1. In YPM 2174 both A-2 and A-3 are double and fused along their dorsal halves, with A-2 contributing most of the medial section; A-4 is divided; A-5, A-6, and A-7 are complete and fused; A-8 and subsequent elements are complete and unmodified. The pessulus is short, extending from between the dorsal ends of A-4 about halfway to the ventral ends of A-3. YPM 1021 differs from YPM 2174 in that A-5, A-6, and A-7 are free. The pessulus is fused to A-5 dorsally and extends to the ventral ends of A-3.

Myiozetetes cayanensis is like *M. similis* (YPM 1543) except as follows. YPM 2024 lacks all fusion. In YPM 1769 A-5 is complete and there is no fusion. The pessulus is fused to the dorsal end of A-4L. In YPM 1844 A-5, A-6, and A-7 are fused and only A-3L is fused to A-2. The pessulus, fused dorsally to A-5, extends only about halfway to the ventral end of A-3. *M. granadensis* is like the "typical" *similis* except that A-4 and A-5 are complete and fused. There is no other fusion and no pessulus.

Musculature.

In *Tyrannus tyrannus* (Pls. 9 and 10), *T. melancholicus,* and *T. dominicensis* the Mm. tracheolaterales converge ventrally at about A-27 (variable) covering the ventral half of the trachea to about A-9, where they diverge slightly. Their insertion lies along a pair of spiral lines from A-4 ventrally to A-6 dorsolaterally. M. sternotrachealis originates on the interior surface of the coracoid process of the sternum. Near its insertion it divides into three fasciculi which insert, respectively, on the ventral portion of the membranous sheath surrounding M. tracheolateralis, in continuity with the lateral fibers of the latter, and dorsolaterally directly on A-10 through A-16, adjacent to the dorsal edge of M. tracheolateralis.

M. obliquus ventralis protrudes strongly on each side of the syrinx. It originates directly on A-3 and A-4 ventrilaterally and on A-4 and A-5 laterally and dorsolaterally, the deeper fibers being attached to the more posterior element. The muscle extends posterodorsad to insert directly on the dorsal tenth of A-1, on the dorsal fifth of B-1, and by a narrow tendon to the center of the B-1/B-2 membrane. The deep fibers are oriented anteroposteriorly, the superficial ones more dorsoventrally.

Tyrannus albogularis is like *T. tyrannus* except that the muscles are less strongly developed.

Müller's brief description of *T. melancholicus* agrees closely with the above. Miskimen's description of *T. tyrannus,* based on three individuals, is quite different from the above. She found M. tracheolateralis inserting on the dorsal end of A-3 ("bronchial bar 2") and on the ventral part of A-5 ("drum"). In describing M. sternotrachealis she stated that it inserts on M. tracheolateralis and on A-11 ("tracheal ring 6"). M. obliquus ventralis she described as above, but without the tendinous insertion to the B-1/B-2 membrane.

Muscivora is like *Tyrannus,* differing as follows. M. tracheolateralis inserts entirely on A-7. M. sternotrachealis is more robust and some of the ventral fibers are continuous between the right and left muscles. The dorsal fasciculus inserts on A-9 through A-14. The Mm. obliqui ventrales touch at the ventral midline. They originate on A-7 superficially, on A-6, and on A-5 deeply and insert superficially on the dorsal half of B-1 and deeply on the dorsal end of A-1.

Miskimen's specimen of *Muscivora* differed from the above in lacking the direct insertion of M. sternotrachealis and the insertion of M. obliquus ventralis on B-1.

Myiodynastes is like *Tyrannus,* differing as follows. The Mm. tracheolaterales are very narrow, do not converge ventrally, and insert on A-6 only. The Mm. sternotracheales are asymmetrical; the right inserts partly directly on A-12 through A-15, on both sides of the ventral midline, and partly in continuity with M. tracheolateralis; the left is wholly continuous with M. tracheolateralis. The Mm. obliqui ventrales are widely spaced ventrally, originating mostly on A-6, with a few superficial fibers attached to A-7 dorsolaterally. They insert on the dorsal third of A-1, adjacent parts of the A-1/A-2 membrane, the dorsal tip of B-1, and the intervening part of the A-1/B-1 membrane.

In my specimen of *Tyrannopsis* much of the syringeal musculature was eaten by ants, but it is certain that the positions of the muscles were as in *Tyrannus*. Evidently the Mm. obliqui ventrales were strongly protruding, to judge from the direction of the remaining fibers.

Megarhynchus is like *Tyrannus*, differing as follows. The Mm. tracheolaterales converge midventrally at A-26 and remain in contact to their insertion, on A-4 and A-5. Most of the fibers of M. sternotrachealis are in the ventral fasciculus, which inserts broadly on the membranous sheath of M. tracheolaterales. M. obliquus ventralis is shorter and broader than in *Tyrannus*. It originates in an elliptical area covering A-5 laterally (superficial fibers), most of A-4, and A-3 laterally (deep fibers). It inserts directly on the dorsal ends of A-1 and B-1, on the A-1/B-1 membrane, and also by a broad thin tendon to the B-1/B-2 membrane and the dorsal end of B-2.

The two species of *Pitangus* differ sharply from each other. *P. sulphuratus* is like *Tyrannus*, differing as follows. M. tracheolateralis is narrow and lateral, inserting on A-4 only. M. sternotrachealis inserts directly on A-13 through A-17. M. obliquus ventralis is broader and thicker than in *Tyrannus*. It originates near the ventral midline on A-3 through A-7 and around to the dorsolateral surfaces of A-5, A-6, and A-7. A few short, deep fibers extend from A-3 to A-2; the remainder of the muscle inserts on the dorsal third of A-1 and B-1, the dorsal tip of B-2, and (a few fibers) on the intervening part of the B-1/B-2 membrane. Müller's description of *P. sulphuratus* agrees closely with the above.

In *P. lictor*, M. tracheolateralis is narrow and lateral and inserts on A-6. M. sternotrachealis has two fasciculi, the ventral one of which, less than a quarter of the muscle, is continuous with M. tracheolateralis. The rest of the muscle inserts directly on A-15 and A-16, at the dorsal edge of M. tracheolateralis. M. obliquus ventralis originates along the ventral midline on A-3 through A-7 and around to the dorsolateral part of A-7; it inserts with a broad tendon to the dorsal third of B-1.

Tolmarchus is like *Tyrannus*, differing as follows. M. sternotrachealis has only two fasciculi, a ventral one inserting on the membranous sheath of M. tracheolateralis, and a dorsal one inserting directly on A-9, A-10, and A-11. M. obliquus ventralis originates along a line from the ventrilateral region of A-4 across A-5 to the dorsolateral region of A-6. It inserts directly on the dorsal end of the B-1/B-2 membrane, with no apparent attachment to the elements themselves.

Conopias is like *Tyrannus*, differing as follows. M. tracheolateralis is narrower and thicker, and situated laterally, inserting on A-5. The left M. sternotrachealis has three fasciculi; the right only two. In the latter, one fasciculus is continuous with M. tracheolateralis, while the other inserts directly on A-13, A-14, and A-15. M. obliquus ventralis originates ventrilaterally on A-4 and dorsolaterally on A-5; it inserts on the dorsal end of B-1, with a few fibers attached to the adjacent membranes.

Empidonomus is like *Tyrannus*, differing as follows. The Mm. tracheolaterales nearly surround the trachea, leaving a very narrow space mid-dorsally and a slightly wider one posterior to their divergence ventrally at A-9. M. sternotrachealis inserts dorsally and ventrally on the membranous sheath surrounding M. tracheolateralis and laterally in continuity with the latter. M. obliquus ventralis originates all along the insertion of M. tracheolateralis. Most of the muscle mass is in the dorsal and dorsolateral regions. It inserts on the dorsal quarter of B-1.

Legatus (Pls. 7 and 8) differs markedly from all of the above. M. tracheolateralis is narrow and lateral, broadening slightly near its insertion, on A-7 and A-6 ventrilaterally and on A-5 dorsolaterally. The thin M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis, on A-11 through A-18. The left M. obliquus ventralis is longer than the right, originating slightly to the right of the ventral midline on A-7 and on the midline of A-6 and A-5. It extends posterolaterally to insert by a tough, transparent tendon to the dorsal end of B-1. The tendon overlies that of M. obliquus lateralis and the two are lightly attached where they pass over A-1. The right muscle originates just to the right of its sibling and inserts in the same manner. M. obliquus lateralis originates on the lateral surface of A-5 and extends posteriad to insert by a broad tendon to the ventral half of B-1.

Myiozetetes (Pls. 9 and 10) is like *Legatus*, differing as follows. In all specimens the Mm. tracheolaterales are very close ventrally but do not touch. In *M. cayanensis*, *M. granadensis* and two specimens of *M. similis* (YPM 1543 and 2174) the insertion is on A-6 ventrally and A-7 laterally. In the third specimen of *M. similis* (YPM 1021) it is on A-5 ventrally and A-6 laterally. M. sternotrachealis is thin in all individuals. It inserts directly on two or three elements in the region of A-14, except in YPM 1024 (*M. cayanensis*), in which the ventral third of the fibers are continuous with the dorsal fibers of M. tracheolateralis. The Mm. obliqui ventrales are symmetrical, originating, in all specimens, along the ventral midline from A-3 to a point just posterior to the insertion of the Mm. tracheolaterales. Each of the oblique muscles extends posterodorsally to insert by a narrow tendon to the dorsal end of A-1. In *M. cayanensis* and in one specimen of *M. similis* (YPM 1021) the ventral half of this muscle inserts on the broad tendon of M. obliquus lateralis. The latter originates just posterior to the lateral insertion of M. tracheolateralis, and inserts by a broad tendon to the ventral half of B-1.

Sirystes is unlike all of the above. M. tracheolateralis, thin and narrow, lies on the ventrilateral surface of the trachea and inserts on the anterior edge of A-5. M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis on A-9, A-10, and A-11. M. obliquus ventralis originates near the ventral midline of A-3, A-4, and A-5 and laterally on A-5. It extends posterodorsally to insert on the center third of A-1. The musculature of YPM 2791 is considerably more slender than that of YPM 2790.

SUBFAMILY MYIARCHINAE.

Specimens Examined.

Of the 78 species in 21 genera (including *Aechmolophus* Zimmer 1938), I have examined the following 34 specimens of 26 species in 16 genera:

Myiarchus crinitus (Linnaeus), three specimens
Myiarchus brachyurus Ridgway
Myiarchus tyrannulus (Müller)
Myiarchus ferox (Gmelin)

Myiarchus tuberculifer (Lafr. and D'Orb.), two specimens
Eribates magnirostris (Gould), two specimens
Nesotriccus ridgwayi Townsend
Nuttallornis mesoleucus (Lichtenstein)
Myiochanes [= *Contopus*] *virens* (Linnaeus), two specimens
Myiochanes cinereus (D'Orbigny)
Blacicus carribaeus (D'Orbigny)
Empidonax flaviventris (Baird)
Empidonax minimus (Baird), three specimens
Empidonax difficilis Baird
Empidonax albigularis Sclater and Salvin
Empidonax oberholseri A. R. Phillips
Aechmolophus mexicanus Zimmer
Cnemotriccus poecilurus (Sclater)
Mitrephanes phaeocercus (Sclater)
Terenotriccus erythrurus (Cabanis)
Aphanotriccus capitalis (Salvin)
Myiobius sulphureipygius (Sclater)
Myiobius atricaudatus Lawrence
Pyrrhomyias cinnamomeus (Lafr. and D'Orb.)
Myiophobus fasciatus (Müller)
Onychorhynchus coronatus (Müller), two specimens

I know of the following descriptions by previous authors:

Myiarchus crinitus (Linnaeus) — MacGillivray (1838, p. 423)
Myiarchus crinitus (Linnaeus) — Miskimen (1963)
Myiarchus stolidus (Gosse) — Maynard (1928, p. 143)
Myiarchus ferox (Gmelin) — Müller (1847, p. 34; 1878, p. 28)
Myiochanes virens (Linnaeus) — MacGillivray (1838, p. 426)
Myiochanes virens (Linnaeus) — Maynard (1928, p. 138)
Myiochanes virens (Linnaeus) — Miskimen (1963)
Empidonax minimus (Baird) — MacGillivray (1838, p. 427)
Empidonax minimus (Baird) — Maynard (1928, p. 135)
Empidonax traillii (Audubon) — Miskimen (1963)
Empidonax virescens (Vieillot) — MacGillivray (1838, p. 427)
Terenotriccus erythrurus (Cabanis) — Müller (1847, p. 35; Pl. 5, fig. 8; 1878, p. 29)

Cartilaginous Elements.

Myiarchus crinitus (Pls. 9 and 10) is typical of the genus. There is considerable variation among my specimens, particularly in the configuration of A-3. In all three A-1 is divided and A-2 is double. In YPM 759 the medial portion of A-2 has a short section of porous white cartilage narrower than the rest of the element. A-3 is divided. A-3R has a medial extension about halfway to the ventral end of the element. This condition is found in both halves of A-3 in the unnumbered specimen, but not at all in YPM 1122. A-4 and other A-elements are complete. In YPM 759 and 1122 A-4 and A-5 are fused, while in the unnumbered specimen it is A-5 and A-6. The B-elements are uniform among my specimens. All are divided and only the dorsal end of B-1 is spatulate. There are two pairs of internal cartilages. The dorsal pair are thick, large and ⅃-shaped with the short arm directed ventrad and the long arm terminating anteriorly near the dorsomedial edge of A-2. The anterior ends of this pair are connected by a cartilaginous plug in the form of a bar at right angles to the sagittal plane. The ventral pair are short, thick bars lying ventral to the short arm of the dorsal pair, and aligned with it. There is no pessulus. *M. brachyurus* is like *M. crinitus* (unnumbered specimen).

M. tuberculifer is also like *M. crinitus*, except as follows. In YPM 1889 the dorsal end of A-3R is connected to A-4 by a short intermediate section and a similar section joins A-4 and A-5 mid-dorsally. In YPM 1040 these connections are lacking, but A-5 and A-6 are fused for about 30° on each side of the ventral midline. *M. ferox* is like *M. crinitus* (unnumbered) differing only in that A-3 is double, the medial portion being narrow and opaque. In addition the dorsal half of A-4 is fused to A-5 and the whole of A-5 to A-6. *M. tyrannulus* is like *M. crinitus,* except that A-1 through A-4 are divided and A-5 is incomplete ventrally. A-4L is fused to A-5 dorsally and to A-5R ventrally, leaving the ventral end of A-5L free. A-6 and A-7 are fused on the left side.

Müller's description and illustration of *M. ferox* agree closely with the above. In *M. stolidus* Maynard described and figured a "syringeal box" of divided elements A-1 through A-4, closely fitted but not fused. He did not mention the pessulus or the internal cartilages. In *M. crinitus* Miskimen found the elements to be like those of my YPM 759, but with A-2 divided and a partial fusion of A-4 and A-5.

Eribates is like *Myiarchus* (unnumbered), differing as follows. A-2 is divided. In USNM 20541 A-4 and A-5 are fused for their dorsal halves. The bridge between the internal cartilages is larger and its junction with the cartilages less distinct. In USNM 223306 the bridge has a ventral extension almost reaching the ventral surface at A-2. The smaller pair of internal cartilages is absent.

Myiophobus is like *Myiarchus,* differing as follows. A-4 and A-5 are divided; A-6 is incomplete dorsally. The pessulus extends in an arc from between the ventral ends of A-5 to the region between A-4 and A-5 mid-dorsally, where it is fused to A-4R and A-5L. The internal cartilages are straight flat bars attached to the dorsomedial region of A-2 and extending posteriad to the level of B-1. The connecting bridge and the smaller pair of internal cartilages are absent.

Terenotriccus (Pls. 11 and 12) is unlike all of the above. A-1 is divided; A-2 and A-3 are double; A-4 is divided; A-5 and other A-elements are complete. There is an extra divided component, A-4aR. The pessulus is fused dorsally to A-4L and extends to the ventral ends of A-4, where it is not fused. The internal cartilages are thin and slightly hooked ventrad. Müller's brief mention of this genus stated only that two elements (A-2 and A-3) are double.

Onychorhynchus is like *Terenotriccus*, differing as follows. In both individuals the extra component is "double" and seems best designated A-3aR. A-4 is incomplete dorsally and is joined ventrally to A-3aR by a midventral extension. The internal cartilages are flat plates in the shape of a two-kerneled peanut, oriented with the long axis dorsoventrally. Each is connected to the respective dorsomedial region of A-2 by a thin strand of cartilage from the dorsal end of the "peanut." In the male specimen the medial side of each plate is covered by a prominent capsule of yellow fat; in the female the fat capsule is much less bulging.

Pyrrhomyias is like *Terenotriccus,* differing as follows. A-2R is divided; A-2L and A-3 are double, A-2L being wholly fused to A-3L. A-4 and A-5 are divided. A-5L and the ventral end of A-5R are fused to A-6. The pessulus is fused to the dorsal midline of A-6 and extends posteriad, then ventrad to the ventral region of A-3 where it is also fused. The internal cartilages are tapering bars, fused to A-3R and A-2L and extending posteriad to the level of B-1.

Myiobius is like *Terenotriccus,* differing as follows. In *M. atricaudatus* A-4 is complete and fused ventrally to A-5. The fusion includes A-4aR. The pessulus is absent, but its place appears to be taken by a broadened medial section of A-3L, occupying a midsagittal position. In *M. sulphureipygius* A-4 and A-5 are incomplete dorsally and A-4 is fused to the ventral end of the pessulus.

Nuttallornis (Pls. 9 and 10) is unlike all of the above. A-1, A-2 and A-3 are divided; A-4 and A-5 are incomplete dorsally. A-4L and A-5L are fused at their dorsal ends. There is no pessulus. The internal cartilages are broad rounded triangles flexibly connected to the dorsal end of A-2 and to the cartilaginous plug. The latter forms a short wall at right angles to the sagittal plane.

Aphanotriccus is like *Nuttallornis,* differing as follows. A-4 and A-5 are complete and unfused. The internal cartilages are not attached to A-elements.

Empidonax is like *Nuttallornis,* differing as follows. The five species differ only in the details of A-elements. In six of the seven individuals A-1 through A-4 are divided and A-5 is complete. In the exception, YPM 700 (*E. minimus*), A-5 is incomplete dorsally, but the dorsal ends are in contact and closely fitted. In all specimens the dorsal ends of the divided elements are curled medially and adjacent elements are closely fitted. The pessulus is variable. In all except YPM 706 (*E. minimus*) and YPM 1544 (*E. oberholseri*) it is a short bar extending from between the dorsal ends of A-4 to the ventral end of that element, closely fitted to adjacent elements at the ends, but not fused. In YPM 706 the pessulus is lacking, but the dorsal ends of A-4 extend about one-third of the distance across the internal tympaniform membrane. In YPM 1544 A-5L has a posteriad and ventrad extension reaching halfway to the ventral part of the element. In all specimens the internal cartilages are J-shaped with the curvature directed ventrad. They are fused anteriorly to a small arched cartilaginous plug.

MacGillivray described the syrinx of *E. minimus* as being like that of *Tyrannus,* with two "dimidiate" (divided) elements, A-1 and A-2, and the rest of the A-elements complete. He found no pessulus. Maynard's description is not readily compared with others, as he provided no reference point. In his specimen the pessulus was present. In *E. traillii* Miskimen found A-4 and A-5 complete and fused, with the pessulus apparently fused to both ends of A-4.

Mitrephanes is like *Nuttallornis,* differing as follows. A-4 is incomplete dorsally and A-5 is complete. A substantial pessulus, mostly covered by a cartilaginous plug, is fused to A-4 ventrally and to A-5 dorsally.

Aechmolophus is like *Nuttallornis,* differing as follows. On my specimen there is an extra divided component on the right, which I will call A-2aR. Only A-4 is incomplete dorsally; A-5 and subsequent elements are complete. A-1 has a strong posteriad extension at the dorsal end, almost touching B-1. The dorsal ends of A-3L and A-4R extend posteriad and are fused together. There is no pessulus. The internal cartilages are straight bars, broadening in a slight T-shape at the posterior ends.

They are in contact at their anterior ends, in the interbronchial region.

Blacicus is like *Nuttallornis*, differing as follows. A-1 through A-4 are divided; A-5 and A-6 are incomplete dorsally. A-5L and A-6L are fused dorsally and jointly extend posteroventrad like a short pessulus, reaching about one-third of the way to their ventral ends.

Myiochanes is like *Nuttallornis*, differing as follows. A-1 through A-4 are divided; A-5 is complete and fused to the dorsal end of a thin pessulus. In the unnumbered specimen of *M. virens* there is an extra component, apparently A-1aR. The internal cartilages are thick bars attached anteriorly to a thin cartilaginous plug, which is fused to the dorsal ends of A-2.

The descriptions of this genus rendered by MacGillivray and by Maynard were too vague for close comparison with the above. MacGillivray stated that A-1 and A-2 were divided and the pessulus was absent, a statement he made of all tyrannids. Maynard did not describe the elements in detail. He found the pessulus present. Miskimen's description differs from the above in that both A-4 and A-5 are complete and that A-4, A-5, and A-6 are "incompletely fused." The pessulus apparently is attached to A-4 dorsally and ventrally.

Nesotriccus is unlike all of the above. A-1 is divided; A-2 and subsequent A-elements are complete. A-2 and A-3 are fused except for a small opening on each side of the dorsal midline. The pessulus is broad and is fused to A-2 at both ends. A pair of sheets of soft cartilage fills the spaces between the dorsal ends of B-1 and A-1 and between A-1 and the dorsomedial region of A-2. Short, pointed internal cartilages are attached to these sheets, adjacent to the dorsal ends of A-1.

Cnemotriccus is unlike all of the above. A-1 is divided. A-2 through A-7 are fused into a drum, slightly flared at the posterior end. The pessulus, laterally compressed, is fused to the drum at both ends. The internal cartilages are slightly rounded triangles floating in the membrane near the dorsal end of B-1.

Musculature.

Among the various species of *Myiarchus* (Pls. 9 and 10) there is considerable variation in the locations of muscle attachments and in the shapes of some muscles. The Mm. tracheolaterales either cover the entire ventral half of the trachea (*M. ferox*, *M. brachyurus, M. tuberculifer*) or have only a narrow space at the ventral midline (*M. crinitus, M. tyrannulus*). In YPM 1868 (*M. ferox*) a narrow slip from the left muscle crosses the ventral midline at A-11 and spirals across the surface of the right muscle to insert with the latter on the ventrilateral surface of A-6. A similar slip in YPM 2047 (*M. tyrannulus*) does not cross the right muscle but lies along its ventral edge to the insertion. M. tracheolateralis inserts on A-5 and A-6 in *M. crinitus* and *M. tuberculifer;* along a line from A-8 ventrally to A-6 laterally in *M. brachyurus;* and along a line from A-10 ventrally to A-6 laterally in *M. tyrannulus*.

M. sternotrachealis inserts directly on the lateral surface of the trachea, at the dorsal edge of M. tracheolateralis, the exact region of insertion being variable without apparent relation to species. The most posterior insertion is on A-11 through A-13 (*M. ferox*), the most anterior on A-15 through A-18 (*M. crinitus*, unnumbered specimen).

In *Myiarchus crinitus*, M. obliquus ventralis originates along the ventral midline on A-3 through A-6, as well as ventrilaterally on A-6 and laterally on A-5. In one specimen (unnumbered) the area of attachment is nearly all on A-6, but in the other two the line undulates, resulting in the muscle having two heads. The attachment is continuous through the "dip" between the heads. The insertion is on the middle third of A-1 in all species. In *M. tuberculifer, M. brachyurus* and *M. tyrannulus* the lateral origin is a smooth line. In *M. ferox* there are three heads, but the "dips" between them are very shallow. The anterior limit of the midventral origin is on A-9 in *M. tyrannulus* and A-8 in *M. brachyurus;* in all others it is on A-6.

Müller's description and illustration of *M. ferox* differed from the above only in that M. tracheolateralis is narrow and lateral. In *M. stolidus* Maynard also found this muscle to be narrow. M. obliquus ventralis appears to be located much more laterally in *M. stolidus,* originating on A-5 laterally and inserting on the dorsal end of A-1. Miskimen described the Mm. tracheolaterales of *M. crinitus* as touching at the ventral midline. She found M. sternotrachealis inserting "on M. tracheolateralis" with some fibers continuous. Her statement concerning the presence of M. obliquus lateralis implied discontinuity in the origins of the muscle masses, but her description of the origins made them seem continuous. The difference between her two-muscled form and my one-muscled specimens appears to be a semantic one, but examination of a larger series of individuals may show that in some individuals or populations there is a discrete M. obliquus lateralis.

Eribates is like *Myiarchus crinitus,* differing as follows. M. tracheolateralis inserts on A-8 ventrally and on A-7 laterally. M. obliquus ventralis originates on A-4 through A-8 midventrally and on A-7 laterally.

Myiophobus is like *Myiarchus crinitus,* differing as follows. M. tracheolateralis covers the entire ventral surface of the trachea posterior to A-31 and inserts on A-6 only. M. obliquus ventralis originates ventrally on A-2 through A-6 and along A-6 to the dorsolateral surface. It inserts directly in A-1 and by a short narrow tendon to the dorsal end of B-1.

Cnemotriccus is like *Myiarchus crinitus,* differing as follows. The Mm. tracheolaterales converge ventrally at A-26 and insert on the anterior edge of A-7. M. sternotrachealis inserts directly on a narrow elliptical area from A-13 to A-18. M. obliquus ventralis originates along the ventral midline from A-4 to A-7 and laterally along A-7, directly posterior to the insertion of M. tracheolateralis. It inserts directly on the center of the A-1/B-1 membrane.

Nutallornis (Pls. 9 and 10) is unlike all of the above. The Mm. tracheolaterales converge at the level of A-12 and cover the ventral two-thirds of the trachea from there to their insertion on A-4 ventrally and on A-5 and A-6 laterally. Their fibers diverge around the insertions of the Mm. sternotracheales. The latter are asymmetrical. The right extends through *M. tracheolateralis* to insert in an elliptical area on the lateral surfaces of A-12 through A-15. The left divides into two fasciculi, a ventral one inserting like the whole right muscle, and a dorsal one inserting adjacent to the dorsal edge of M. tracheolateralis, on A-12 through A-16. The Mm. obliqui ventrales originate on a median raphe attached to the ventral ends of A-3 and to the midventral region of A-4 and A-5. The insertion is on the middle fifth of A-1. M. obliquus lateralis (absent in those genera described below as similar to this one) is a narrow band originating on the dorsolateral surface of A-6 and extending posteroventrally to insert on A-1, just dorsal to the insertion of M. obliquus ventralis.

Myiochanes is like *Nuttallornis*, differing as follows. M. tracheolateralis extends further posteriad, inserting on A-2. A few lateral fibers insert on A-1. M. sternotrachealis divides into two fasciculi, a dorsal one extending through M. tracheolateralis to insert directly on A-12 through A-14 and a ventral one across the surface of M. tracheolateralis, inserting on the membranous sheath of that muscle. The raphe of M. obliquus ventralis attaches to A-2 through A-6. Its area of insertion on A-1 is longer than in *Nuttallornis.*

MacGillivray described *Myiochanes* as like *Tyrannus* and *Empidonax,* but his description was concerned only with generalities. Maynard's description is equally generalized. Miskimen's description differs from the above in several ways. In her specimens M. tracheolateralis inserted on A-6; M. sternotrachealis inserted ventrally "on M. tracheolateralis," with no dorsal insertion; M. obliquus ventralis was like the above, except that the origin was directly on the cartilaginous elements.

Empidonax is like *Nuttallornis,* differing as follows. The Mm. tracheolaterales are asymmetrical. As well as covering the left ventral quarter of the trachea, the left muscle extends about 15° to the right of the ventral midline. At the level of A-6 it divides into two fasciculi, one inserting midventrally on A-3 and A-4 and the other inserting laterally on A-1. In *E. difficilis* and *E. albogularis* some fibers insert ventrilaterally on A-5. The right muscle has only the lateral insertion. M. sternotrachealis inserts directly on the lateral surface of the trachea adjacent to the dorsal edge of M. tracheolateralis. The insertion is on A-10 through A-12 in *E. minimus;* on A-14 through A-17 in *E. flaviventris;* on A-12 through A-15 in *E. difficilis;* and on A-11 through A-15 in *E. albogularis* and *E. oberholseri.* M. obliquus ventralis originates on a median raphe continuous with the connective tissue between the ventral ends of A-2 and A-3. The raphe extends anteriorly to the level of A-6 but is not attached; at that level the raphe and its attached muscles overlie the left M. tracheolateralis. The insertion of M. obliquus ventralis is on the posterior edge of A-1.

MacGillivray's and Maynard's descriptions of *Empidonax minimus* are too superficial for close comparison with the above, although there are no points of disagreement. Miskimen's description of *E. traillii* differs in that she found M. tracheolateralis inserting on A-5, with a lateral extension to A-1; M. sternotrachealis inserting "on M. tracheolateralis," as well as directly on A-11 and A-12; the origin of M. obliquus ventralis direct, not by raphe.

Blacicus is like *Nuttallornis,* differing as follows. M. tracheolateralis inserts on A-2 ventrally and on A-1 laterally. M. sternotrachealis inserts directly on A-11 through A-13, adjacent to the dorsal edge of M. tracheolateralis. The raphe of M. obliquus ventralis is attached to the connective tissue between the ventral ends of A-3 and A-4 only. The muscle inserts along most of the ventral half of A-1.

Mitrephanes is like *Nuttallornis,* differing as follows. The Mm. tracheolaterales insert mainly on A-2 and A-3, with a few lateral fibers attached to A-13. M. sternotrachealis inserts directly on A-12 and A-13. The Mm. obliqui ventrales originate on a small piece of cartilage which, in turn, is attached to A-2 and A-3 on both sides of the ventral midline. This peculiar cartilage consists of a small triangular plate attached to the elements by two thin stalks. The two attaching stalks pass between the fibers of the Mm. tracheolaterales. The intrinsic muscle inserts on the middle third of A-1.

Aphanotriccus is like *Nuttallornis,* differing as follows. The Mm. tracheolaterales are separated by a midventral space of about 10° of tracheal circumference.

They insert on A-2. M. sternotrachealis inserts directly on A-13 through A-26, with about one-twentieth of the fibers continuous with M. tracheolateralis. The anterior tenth of the fibers of the Mm. obliqui ventrales are continuous between the pair. The insertion covers the ventral two-thirds of A-1, extending dorsally beyond the edge of M. tracheolateralis.

Aechmolophus is like *Nuttallornis*, differing as follows. The Mm. tracheolaterales insert on A-2, passing beneath the intrinsic muscles, and at their dorsal edges, on A-1. The Mm. sternotracheales insert on the ventrilateral surfaces of the Mm. tracheolaterales at the level of A-10 through A-12. The insertion of M. obliquus ventralis covers nearly the entire ventral half of A-1.

Nesotriccus is unlike all of the above. The Mm. tracheolaterales are quite narrow, each having a width of about 30° of tracheal circumference. They are separated ventrally by a space of about the same width. Their insertion is on A-3 ventrally and on A-2 and A-3 laterally. The right M. sternotrachealis inserts directly on A-8 through A-11, and also with about one-fifth of its fibers in continuity with M. tracheolateralis. The left muscle is similar, except that it reaches A-12 and has a narrow and extremely thin band of fibers extending across the ventral midline to insert on the surface of the right M. tracheolateralis. The band is probably an individual peculiarity of this specimen. Each of the Mm. obliqui ventrales originates adjacent to the ventral midline of A-2, A-3 and A-4. It extends laterally and posterodorsally to insert directly on A-1 (a few deep ventral fibers), by a broad thin tendon to the middle third of B-1 (a few superficial ventral fibers) and by a strong narrow tendon to the subterminal dorsal fifth of B-1 (the major part of the muscle).

Terenotriccus (Pls. 11 and 12) is unlike all of the above. M. tracheolateralis is narrow and ventrilateral, inserting directly on the ventral half of A-1, except the terminal sixth of the element. M. sternotrachealis inserts directly on A-10 through A-12, adjacent to the dorsal edge of M. tracheolateralis. There are no intrinsic muscles. Müller's description and illustrations agree closely with the above.

Pyrrhomyias is like *Terenotriccus*, differing as follows. The Mm. tracheolaterales converge ventrally at A-45 but diverge at A-11. A few fibers on the dorsal edge of each muscle are lightly attached to A-9 and A-10. The insertion is by a broad tendon to the middle third of B-1. The left M. sternotrachealis inserts on A-12 through A-15, the right on A-12 through A-14.

Myiobius is like *Terenotriccus*, differing as follows. The deep fibers of M. tracheolateralis are attached to A-5, so lightly that the connection was severed in dissection, without apparent damage to the muscle fibers. M. sternotrachealis inserts on A-11 through A-14.

Onychorhynchus is like *Terenotriccus*, differing only in that M. sternotrachealis is wholly continuous with the dorsal superficial fibers of M. tracheolateralis, which it touches at A-11.

SUBFAMILY PLATYRINCHINAE.

Specimens Examined.

Of 18 species in five genera, I have examined the following seven specimens of six species in three genera:

Platyrinchus mystaceus Vieillot
Platyrinchus cancrominus Sclater and Salvin
Tolmomyias sulphurescens (Spix), two specimens
Tolmomyias megacephalus (Swainson)
Rhynchocyclus olivaceus (Temminck)
Rhynchocyclus brevirostris (Cabanis)

I know of no descriptions by previous authors.

Cartilaginous Elements.

In *Platyrinchus* (Pls. 11 and 12) A-1, A-2, and A-3 are divided; A-4 is incomplete dorsally; A-5 and subsequent elements are complete. A large pair of internal cartilages extends from the dorsal end of the interbronchial region posteriad to the level of the dorsal end of B-1. The pair are thoroughly fused at their anterior ends, where they are also fused to a small bony disc lying on the dorsal midline. The dorsal ends of A-2 and A-3 are fused to the internal cartilages, but not those of A-1 and A-4. A narrow cartilaginous bar extends posteriad from the posterior end of each of the internal cartilages to the level of B-2, where it bends ventrad and extends nearly to the ventral edge of the internal tympaniform membrane. B-1 is more robust than the other B-elements and lacks the spatulate ends characteristic of them. There is no pessulus.

The two species of *Tolmomyias* are quite different from each other and from *Platyrinchus*. In *T. sulphurescens* (Pl. 20) A-1 is divided; A-2 and A-3 are double and fused along their medial sections. A-4 is incomplete dorsally and A-5 and the remaining A-elements complete. The pessulus is a mid-dorsal posteriad extension of A-5, bending ventrad and extending nearly to the ventral side. In one specimen (YPM C-244) the dorsal end of A-4L is fused to the pessulus. In the same specimen A-7 and A-8 are fused for their ventral halves. There is no fusion in YPM C-535. The internal cartilages are approximate triangles fused to the posterior medial edge of A-2. The B-elements are delicate, nonspatulate, and each except B-1 has an ossified cap on its middle third.

Tolmomyias megacephalus differs from *T. sulphurescens* as follows. A-1 through A-4 are divided and unfused. Due to shot damage some details of the mid-dorsal region are difficult to determine. The pessulus is present, but does not appear to be attached to A-5. There are two pairs of internal cartilages, a long dorsal pair fused to the dorsal ends of A-1 and extending posteriad to the level of B-5; and a ventral pair in the form of rounded squares floating in the membrane. B-1 is broader, thicker, and straighter than the other B-elements and lies very close to A-1.

Rhynchocyclus (Pls. 11 and 12) differs strongly from all of the above. In *R. brevirostris* A-1 through A-4 are divided and lie in planes tilted at about 45° to the tracheal axis. A-5 and subsequent elements are complete. A narrow mid-dorsal extension of the pessulus extends anteriad nearly to A-5. The internal cartilages consist of two pairs, both free. The dorsal pair is slender, slightly S-shaped, and extends from the region of the dorsal ends of A-2 to the ends of B-1. The ventral pair is shield-shaped and lies adjacent to the ventral ends of A-3. *R. olivaceous* differs from *R. brevirostris* in that A-1 is slightly softer, A-4 is double, and the pessulus extends to and is fused with A-5.

Musculature.

In *Platyrinchus mystaceus* M. tracheolateralis covers the ventral half of the trachea from about A-30 posteriad. It inserts by a very thin, transparent, broad tendon to A-1, just ventral of the center of the element. Some of the superficial lateral fibers of M. tracheolateralis are continuous with the ventral half of the M. sternotrachealis, which branches off from the trachea at A-12. The dorsal fibers of M. sternotrachealis insert on the lateral surfaces of A-15 through A-21. M. obliquus ventralis is very narrow, originating on the ventral surface of A-11, with a few fibers continuous with the deep lateral fibers of M. tracheolateralis. It extends posterodorsad to insert by a short narrow tendon on the dorsal tip of B-2. *P. cancrominus* is the same except that M. tracheolateralis inserts atendinously on A-1.

Rhynchocyclus differs sharply from *Platyrinchus*. M. tracheolateralis is a narrow band extending down the ventrilateral surface of the trachea, broadening slightly near its insertion, on A-3. M. sternotrachealis is robust (about one-third of the tracheal diameter) and inserts directly on an elliptical area on the lateral surfaces of A-5 through A-8 in *R. brevirostris* and A-6 through A-12 in *R. olivaceus*. M. obliquus ventralis originates on a median raphe attached to A-4 and A-5 in *R. brevirostris* and to A-5 and A-6 in *R. olivaceus*. It inserts directly in the middle of A-1 in both species.

The two species of *Tolmomyias* differ from all of the above and from each other. In *T. sulphurescens*, M. tracheolateralis consists of a narrow band on the lateral surface of the trachea, inserting on A-6 and A-7 on the left and A-7, A-8, and A-9 on the right. The line of its insertion follows closely the anterior edge of M. sternotrachealis. The latter inserts in a circular area on A-5, A-6, and A-7 on the left and A-6 through A-9 on the right. The single intrinsic muscle, which is most like M. obliquus lateralis of other genera, appears as a continuation of M. tracheolateralis, originating on A-5, at the posterior edge of M. sternotrachealis and extending posteriad to insert near the center of A-1.

In *Tolmomyias megacephalus* the Mm. tracheolaterales meet at the ventral midline at A-6. The insertion of each muscle is in three parts: the ventral half of the fibers inserts directly on A-4; the middle sixth of the fibers extends posteriad to A-2, where its insertion is beneath the intrinsic muscles; the dorsal third of the fibers inserts on the dorsolateral surface of A-5. M. sternotrachealis inserts directly on the lateral surfaces of A-11 and A-12 at the dorsal edge of M. tracheolateralis. M. obliquus ventralis originates on A-3 near the ventral midline and ventrilaterally on A-4 and extends posterolaterally to insert on A-1 just ventral to the center. M. obliquus lateralis originates dorsolaterally on A-5 and extends posteroventrally to insert on A-1, adjacent to the insertion of M. obliquus ventralis.

SUBFAMILY EUSCARTHMINAE.

Specimens Examined.

There are 77 species in the 25 genera recognized by Hellmayr (1927), to which I have added the two species of the genus *Corythopis*, usually included in the Conopophagidae. The inclusion of *Corythopis* in this subfamily is highly tentative, but it certainly belongs in the Tyrannidae (see Ames et al., 1968). I have examined the following 28 individuals of 19 species in 15 genera:

Todirostrum cinereum (Linnaeus)
Todirostrum sylvia (Demarest), two specimens
Todirostrum plumbeiceps Lafresnaye
Oncostoma cinereigulare (Sclater)
Euscarthmornis margaritaceiventer (Lafr. and D'Orb.)
Lophotriccus pileatus (Tschudi), two specimens
Colopteryx galeatus (Boddaert)
Myiornis auricularis (Vieillot), two specimens
Hemitriccus diops (Temminck)
Pogonotriccus eximius (Temminck), two specimens
Leptotriccus sylviolus Cab. and Heine, two specimens
Phylloscartes ventralis (Temminck)
Capsiempis flaveola (Lichtenstein)
Euscarthmus melorhyphus Wied
Corythopis delalandi (Lesson), three specimens
Corythopis torquata Tschudi, two specimens
Pseudocolopteryx sclateri (Oustalet)
Pseudocolopteryx flaviventris (Lafr. and D'Orb.)
Habrura pectoralis (Vieillot), two specimens

I know of only the following descriptions by previous authors:

Todirostrum cinereum (Linnaeus) — Müller (1847, p. 36; 1878, p. 30)
Todirostrum poliocephalum (Wied) — Müller (1847, p. 36; 1878, p. 30)
Lophotriccus sp. — Müller (1847, p. 36; 1878, p. 30)
Colopteryx galeatus (Boddaert) — Müller (1847, p. 36; Pl. 4, figs. 1-3; 1878, p. 29)
Pogonotriccus eximius (Temminck) — Ames et al. (1968)
Corythopis delalandi (Lesson) — Ames et al. (1968)
Corythopis torquata Tschudi — Ames et al. (1968)

The description of the syrinx of *Corythopis* cited above was based on the dissections made in the present study.

Cartilaginous Elements.

In *Myiornis,* minor differences exist between the two specimens. In YPM 2727, A-1 and A-2 are divided; A-3 through A-7 are incomplete dorsally; A-8 and the remaining A-elements are complete, but in YPM 2725 A-3 is divided and A-8 and A-9 are incomplete dorsally. The pessulus in both specimens is a narrow flat plate, extending posteriad from between the ends of the most anterior dorsally incomplete element to the level of A-3, where it curves ventrad. The pessulus of YPM 2727 is fused midventrally to A-3; in YPM 2725, it is fused to the ventral end of A-3R. The B-elements are divided. The internal cartilages are nearly straight and are broadened, flattened, and slightly pointed at the posterior ends. Anteriorly they are flexibly attached to a transverse "horseshoe" of cartilage that partly encloses the pessulus.

Lophotriccus is like *Myiornis,* differing as follows. A-3 and A-4 are divided; A-5 through A-11 are incomplete dorsally. Both specimens are badly shot-damaged, obscuring the configuration of the internal cartilages. The tranverse "horseshoe" is absent. The pessulus is fused midventrally to A-5. The trachea from A-8 to the larynx is much enlarged, particularly in the dorsoventral direction. Its long diameter at A-24 is about 2.5 times that at A-8. Müller's description of the syrinx of *Lophotriccus* agrees with the above, except that in his specimen only A-5 through A-9 were incomplete dorsally.

Euscarthmornis is like *Myiornis,* differing as follows. A-1 through A-6 are divided; A-7 through A-13 are incomplete dorsally. The anterior part of the pessulus is mostly spongy white cartilage, with four irregularly shaped bony plates spaced between A-6 and A-13, varying in diameter from one to three times the width of the A-elements. The dorsal ends of A-1 through A-4 are fused to an inverted "V" of cartilage, continuous with the pessulus. The latter is fused midventrally to A-7.

Colopteryx (Pls. 13 and 14) is like *Myiornis,* differing as follows. A-1 through A-4 are divided; A-5 through A-12 are incomplete dorsally. The dorsal extension of the pessulus stops at the level of the A-10/A-11 membrane, but an additional bony plate lies between the dorsal ends of A-12. Müller's specimen was identical with the above except that the dorsally incomplete section extended through A-16 and the pessulus was continuous to A-16.

Hemitriccus is like *Myiornis,* differing as follows. A-1 through A-5 are divided; A-6 through A-14 are incomplete dorsally. The pessulus extends anteriad to the level of the A-7/A-8 membrane and is fused midventrally to A-6. The region between the dorsal ends of A-8 through A-14 is membranous, except for bony discs at the levels of the A-8/A-9, A-10/A-11 and A-11/A-12 membranes and of A-14. The dorsal ends of A-1 through A-4 are connected by an inverted "V" of cartilage.

Oncostoma is like *Myiornis,* differing as follows. A-1 through A-4 are divided; A-5 through A-22 are incomplete dorsally. The latter have only a slight turning-in at the dorsal ends. The mid-dorsal plate is about twice the width of the A-elements. Anterior to A-12 it is broken up into six sections which, although separate, are closely fitted at their edges. The pessulus is fused midventrally to A-4. There is no cartilage connecting the lower A-elements, nor are there any internal cartilages.

Habrura is unlike all of the above. A-1 is divided; A-2 is incomplete ventrally; A-3 and subsequent A-elements are complete. An extra divided component, A-3aR, is fused dorsally and ventrally to A-3. A-2 is very broad dorsally and blends imperceptably into a broad pessulus, which is narrow and free at its ventral end. In USNM 227218, A-3 is broadly fused dorsally to A-2. The internal cartilages are straight bars, flexibly fused to A-2 and extending posteriad to the level of A-2.

Capsiempis is like *Habrura,* differing as follows. The extra component is lacking. A-3 is connected to A-4 and A-4 to A-5 by narrow mid-dorsal sections. The internal cartilages taper to extremely thin sheets at their posterior ends, blending gradually into the surrounding membranes.

Pseudocolopteryx is like *Habrura,* differing as follows. The extra component is lacking. In *P. flaviventris* A-2 through A-4 are completely fused. In *P. sclateri* fusion has so obscured the edges of the elements that their number is uncertain. About five elements, A-2 through A-6, appear to be involved.

Pogonotriccus is unlike all of the above. A-1 through A-3 are divided; A-4 and subsequent elements are complete. The pessulus is a ventral continuation of a mid-dorsal plate which is fused to A-4 and to the dorsal ends of A-3. The internal cartilages are narrow, straight, tapering bars fused anteriorly to A-3 and extending posteriad to the level of A-1. Ames et al. provide an illustration (but no description) based on the two specimens described here.

Phylloscartes is unlike all of the above. A-1 and A-2 are divided; A-3 is double; A-4 and subsequent A-elements are complete. The medial sections of A-3 are fused for their ventral two-thirds and join the ventral surface of the element as a single narrow strip. A-2R is fused dorsally to A-3R. The internal cartilages are straight, narrow bars, fused to the dorsomedial regions of A-3.

Leptotriccus is unlike all of the above. A-1 and A-2 are divided. In YPM 2694, A-3 is divided; A-4 and subsequent elements are complete. In YPM 2693, A-3 is double; A-4 and A-5 are incomplete dorsally. In the first specimen the pessulus is a narrow bar fused to the mid-dorsal region of A-4 and extending about halfway to the ventral surface; in the second it is fused dorsally to A-4L and ventrally to both components of A-3. In the latter individual A-2R is fused dorsally to A-3R and the whole of A-5L to A-6. The internal cartilages in YPM 2694 are long rounded bars joined by a narrow neck to the dorsal ends of A-2; in YPM 2693 they are small hemispheres connected to A-2 by a narrow strand of cartilage.

Todirostrum (Pls. 11 and 12) is unlike all of the above. In *T. sylvia* A-1 through A-6 are divided; A-7 and subsequent A-elements are complete. In YPM 1070 the pessulus is a straight bar free at both ends; in YPM 1763 it is fused to A-6L at both ends. The divided A-elements extend about one-third of the way across the internal tympaniform membranes from the dorsal side and are fused to the dorsal internal cartilages, thin plates occupying the center thirds of the membranes. The ventral pair are small hemispheres attached to the ventral ends of B-2 and B-3. *T. cinereum* is like *T. sylvia*, except that only A-1 through A-4 are divided, the remaining A-elements being complete. A-5 and A-6 are fused about 30° to the left of the dorsal midline. *T. plumbeiceps* is like *T. sylvia* except that A-1 through A-5 are divided. Müller's descriptions of *T. cinereum* and *T. poliocephalum* agree with that of *T. cinereum*, above.

Euscarthmus is unlike all of the above. A-1 and A-2 are divided; A-3 and A-4 are incomplete dorsally; the remaining A-elements are complete. A-5 through A-9 are about twice the width of the other A-elements and are fused into a rigid cylinder (Pl. 20). The dorsal end of A-4L is fused to A-5. The pessulus is fused dorsally to A-3L, A-4L and A-5 and ventrally to A-4. The internal cartilages are straight tapered bars extending from the dorsal ends of A-3 to the level of B-2.

Corythopis is unlike all of the above. A-1 and A-2 are divided; A-3 and subsequent elements are complete. A-3 and A-4 are fused for about 15° on each side of the dorsal and ventral midlines, producing a short rigid drum. A robust pessulus, wide dorsally and narrow ventrally, is fused to A-3 at both ends. The internal cartilages are slightly flattened spheres lying in the internal tympaniform membranes at the level of B-4. Connecting each sphere with the respective dorsal end of A-2 are two narrow ribbons of cartilage, also lying in the membrane. B-1 is extremely heavy, its maximum width being about three times that of most A-elements. Its dorsal ends are slightly tapered and not flattened.

Musculature.

In *Oncostoma,* M. tracheolateralis is located on the ventrilateral surface of the trachea, inserting on A-10 and A-11. The lateral fibers are continuous with M. sternotrachealis. The whole of the latter muscle is continuous with M. tracheolateralis, which it meets at A-12. The right M. obliquus ventralis originates on A-9 and A-10 slightly to the left of the ventral midline and extends posterodorsad to insert in a narrow area near the dorsal end of B-1R. The left muscle originates on the right ventrilateral region of A-9 and A-10 and inserts near the dorsal end of B-1L. In the region of overlap each muscle divides into three layers which alternate, the deepest layer belonging to the right muscle, the most superficial to the left muscle. M. obliquus lateralis originates on the lateral surfaces of A-7 through A-9 and inserts on B-1 just dorsal to the insertion of M. obliquus ventralis.

Colopteryx (Pls. 13 and 14) is like *Oncostoma,* differing as follows. At A-15 M. tracheolateralis divides into two fasciculi, which extend dorsal and ventral to the insertion of M. sternotrachealis. The dorsal branch inserts on the dorsolateral surfaces of A-10 and A-11. The ventral fasciculus of the left muscle covers an area about 15° on both sides of the ventral midline and inserts in a narrow area on the ventral midline of A-5. The ventral fasciculus of the right muscle is much narrower than that of the left and inserts ventrilaterally on A-11. M. sternotrachealis inserts directly on the lateral surfaces of A-10 through A-15. M. obliquus ventralis originates ventrilaterally on A-10 and A-11 and extends superficial to the M. tracheolateralis. The number of layers in the region of crossing is difficult to determine, due to their thinness and the brittle quality of the fibers in my specimen. It appears to be about six for each muscle. M. obliquus lateralis originates on A-6 through A-8.

Müller's description and illustration of *Colopteryx* agree with the above except that he described a midventral azygous ("unpaariger") muscle which seems to correspond to the ventral fasciculus of the left M. tracheolateralis, but which is illustrated as being discontinuous with the rest of that muscle. The illustration shows the azygous muscle lying superficial to the Mm. obliqui ventrales.

Lophotriccus is like *Oncostoma,* differing as follows. M. tracheolateralis inserts on A-8 ventrilaterally and on A-5 dorsolaterally. M. sternotrachealis inserts on the lateral surfaces of A-7 through A-10. M. obliquus ventralis originates ventrilaterally on A-7 and A-8. In USNM 428193 the posterior fibers of the deepest muscle layer are continuous between the pair of muscles. M. obliquus lateralis originates laterally on A-6, immediately anteroventral to the insertion of M. tracheolateralis. Müller's brief description of *Lophotriccus* agrees completely with the above.

Euscarthmornis is like *Oncostoma,* differing as follows. The left M. tracheolateralis divides into three fasciculi. The ventral branch attaches midventrally to A-13, the middle one to the ventrilateral surfaces of A-8 and A-9, and the dorsal one to the dorsolateral surface of A-7 through A-9. Some superficial fibers of the middle fasciculus are continuous with those of M. sternotrachealis. In the right M. tracheolateralis the ventral branch inserts midventrally on A-14, beneath the subterminal part of the right muscle. The entire dorsal fasciculus is continuous with M. sternotrachealis. The Mm. sternotracheales insert only in continuity with the previous muscle. In the Mm. obliqui ventrales the deeper layers are situated more posteriorly. The combined origins of the pair of muscles cover most of the ventral and ventrilateral surfaces of A-8 through A-11. M. obliquus lateralis originates on the lateral surfaces of A-8 and A-9 and inserts on B-1 just anterior to the insertion of M. obliquus ventralis.

Myiornis is like *Oncostoma*, differing as follows. M. tracheolateralis divides into two fasciculi which pass respectively ventral and dorsal to the insertion of M. sternotrachealis. The ventral fasciculus inserts on A-10 ventrally and on A-9 ventrilaterally; the dorsal one inserts on A-5 dorsolaterally. M. sternotrachealis inserts directly on the lateral surfaces of A-7 through A-13. The Mm. obliqui ventrales are asymmetrical. The left originates on both sides of the ventral midline of A-8 and ventrilaterally left on A-9 and A-10; the right originates on both sides of the ventral midline of A-9 and ventrilaterally right on A-10. The right muscle extends superficially across the left. Both muscles insert near the respective dorsal ends of B-1. M. obliquus lateralis originates on the lateral surface of A-6 and inserts on B-1, just dorsal to the insertion of M. obliquus ventralis.

Hemitriccus is like *Oncostoma*, differing as follows. The Mm. tracheolaterales are asymmetrical. The left muscle has three areas of insertion: on the dorsolateral surfaces of A-7 and A-8, in the center of B-1, and (crossing the ventral midline) on the ventral end of A-5R. The right muscle inserts only on A-7, A-8, and B-1. M. sternotrachealis inserts on a series of small areas on the lateral surfaces of A-9 through A-16. The insertion on each element extends ventrad a little further than that on the element posterior to it. M. obliquus ventralis is present on the left side only, originating midventrally on A-8 and inserting on B-1 just ventral to the attachment of M. tracheolateralis. M. obliquus lateralis originates on the dorsolateral surfaces of A-7 through A-13. There are only a few fibers attached to each element from A-9 through A-13, for they share the surface of the element with the fibers of M. sternotrachealis.

Habrura is unlike all of the above. The Mm. tracheolaterales converge at the level of A-10 and cover the ventral half of the trachea from there to their insertion on the anterior edge of A-3. M. sternotrachealis inserts directly on the lateral surfaces of A-8 through A-11. M. obliquus ventralis originates on the posterior edge of the ventral half of A-3 and inserts on the center of the A-1/B-1 membrane. M. obliquus lateralis is absent.

Capsiempis is like *Habrura*, differing as follows. M. tracheolateralis inserts on the ventral and ventrilateral surfaces of A-5. M. obliquus ventralis originates near the ventral midline of A-4 and A-5 and ventrilaterally on A-5. It inserts both on A-1 and on the A-1/B-1 membrane.

Phylloscartes is unlike all of the above. The Mm. tracheolaterales converge ventrally at the level of about A-26, covering the ventral surface of the trachea from there to their insertion, ventrally and ventrilaterally on A-4 and laterally on A-3. M. sternotrachealis inserts directly on the lateral surfaces of A-10 through A-14 adjacent to the dorsal edge of M. tracheolateralis. M. obliquus ventralis originates along the ventral quarter of A-4 and inserts in the center of the A-1/B-1 membrane. A narrow M. obliquus lateralis originates on the lateral surface of A-3 and inserts on the A-1/B-1 membrane, just dorsal to the insertion of M. obliquus ventralis.

Pseudocolopteryx is like *Phylloscartes*, differing as follows. M. tracheolateralis inserts on A-4 ventrally, on A-2 ventrilaterally and on A-4 laterally. M. sternotrachealis inserts directly on A-13 through A-17. In addition, some of its anterior fibers are continuous with those of M. tracheolateralis. The Mm. obliqui ventrales originate on a midventral raphe attached to A-3 through A-5 and insert on the ventral third of A-1. M. obliquus lateralis originates on the lateral surface of A-4 and inserts on A-1, just dorsal to the insertion of M. obliquus ventralis.

Pogonotriccus is unlike all of the above. The Mm. tracheolaterales converge at about the level of A-27 and cover the ventral third of the trachea to their insertion on A-5. M. sternotrachealis inserts directly on the lateral surfaces of A-10 through A-14. M. obliquus ventralis originates on a raphe attached to A-4 and A-5 slightly to the right of the ventral midline. It inserts by a broad thin tendon to the dorsal end of B-1.

Euscarthmus is like *Pogonotriccus*, differing as follows. M. tracheolateralis inserts on A-3 ventrally and on A-2 ventrilaterally and laterally. M. sternotrachealis inserts on A-8 through A-13. The raphe of M. obliquus ventralis is attached to A-2 and A-3. The muscle inserts directly on the center third of B-1.

Leptotriccus is unlike all of the above. The Mm. tracheolaterales converge ventrally at the level of A-20 and diverge slightly at A-6 to insert ventrilaterally and laterally on A-3. M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis on A-15 through A-21. M. obliquus ventralis originates on the ventral ends of A-2 (YPM 2694 only) and A-3, midventrally on A-4. It inserts near the center of the A-1/B-1 membrane. In YPM 2693 the posterior third of the fibers are continuous between the two muscles, without midventral attachment. M. obliquus lateralis originates on the lateral surface of A-3 and inserts on the A-1/B-1 membrane, just dorsal to the insertion of M. obliquus ventralis.

Todirostrum (Pls. 11 and 12) is unlike all of the above. M. tracheolateralis is a thin narrow, lateral muscle that divides into two fasciculi at the level of A-12 in *T. sylvia* and *T. cinereum* and A-11 in *T. plumbeiceps*. The fasciculi extend dorsal and ventral, respectively, to the insertion of M. sternotrachealis and insert on A-6 in *T. sylvia*, on A-7 in *T. cinereum*, and on A-5 in *T. plumbeiceps*. M. sternotrachealis inserts on A-8 through A-11 in *T. sylvia* and *T. cinereum*, and on A-7 through A-11 in *T. plumbeiceps*. The proper name for the intrinsic muscle is uncertain, but its position corresponds most closely to that of M. obliquus lateralis of other species. It originates laterally on A-6 in *T. sylvia*, on A-7 in *T. cinereum* and on A-5 in *T. plumbeiceps*. Its width at the origin is the same as that of the insertion of M. tracheolateralis in all specimens except YPM 1070 (*T. sylvia*), in which the intrinsic muscle is about one-third narrower, the difference being at the dorsal edge. It extends posteriad to insert on the center third of B-1.

Müller's description of *Todirostrum* is similar to the above except that he did not find an intrinsic muscle. He described M. tracheolateralis as extending to B-1.

Corythopis is unlike all of the above. The Mm. tracheolaterales converge ventrally at the level of A-14 and remain in contact to their insertion, on the ventral third of A-4. M. sternotrachealis is very thick, its diameter being about one third that of the trachea, and it inserts directly on the lateral surfaces of A-7 through A-10, adjacent to the dorsal edge of M. tracheolateralis. The Mm. obliqui ventrales originate on a median raphe attached to A-3 and A-4, slightly to the right of the ventral midline. Each muscle extends laterad and then posterodorsad to insert in the center of the A-1/B-1 membrane.

SUBFAMILY SERPOPHAGINAE.

Specimens Examined.

Of 25 species in 9 genera, I have examined the following 11 individuals of 7 species in 7 genera:

Tachuris rubrigastra (Vieillot), four specimens
Spizitornis parulus (Kittlitz)
Stigmatura budytoides (Lafr. and D'Orb.)
Serpophaga subcristata (Vieillot)
Inezia subflava (Scl. and Salv.)
Mecocerculus leucophrys (Lafr. and D'Orb.), two specimens
Colorhamphus parvirostris (Darwin)

I know of no descriptions by previous authors.

Cartilaginous Elements.

In *Serpophaga* A-1 is divided; A-2 and A-3 are double; A-4 and subsequent elements are complete. A-2 through A-5 are fused dorsally and A-3 and A-4 are also fused ventrilaterally, The fused medial sections of A-2 and A-3 form a continuous central plate. All of the B-elements are divided. The internal cartilages are narrow bars slightly curved dorsad, their anterior ends flexibly attached to the dorsomedial region of A-2 and to the dorsal end of A-1.

Spizitornis is like *Serpophaga,* differing as follows. A-2L and A-3L are fused laterally; A-3 and A-4 are broadly fused ventrally. The dorsal fusion of A-2 and A-3 and of A-3 and A-4 consists only of a narrow mid-dorsal region.

Mecocerculus is like *Serpophaga,* differing as follows. A-2 is divided and is fused to A-3 at its dorsal ends. The medial sections of A-3 are fused, forming a plate that is broad dorsally and narrow ventrally. A-5 is in contact with A-4 laterally but they are not fused. The internal cartilages are straight, are broader than those of *Serpophaga* and are constricted into a narrow neck near their attachment to A-2.

Colorhamphus is unlike all of the above. A-1 is divided; A-2 and subsequent elements are complete. A-2 and A-3 are joined by a narrow mid-dorsal plate. The pessulus is fused to A-2 at both ends. The internal cartilages are narrow rounded triangles flexibly attached to A-2 and extending posteriad to the level of B-1.

Inezia is unlike all of the above. A-1 and A-2 are divided; A-3 is double; A-4 and subsequent elements are complete. A-5 and A-6 are fused for about 15° on each side of the dorsal and ventral midlines. There is no pessulus. There are two pairs of internal cartilages. The usual dorsal pair are straight bars, fused to the dorsomedial region of A-3 and extend to the level of B-1, where they are flattened and terminally indented. The ventral pair are thin round discs fused to the ventrimedial region of A-3.

Tachuris (Pls. 13 and 14) is unlike all of the above. In three specimens (YPM 3, 2796, 2799) A-1 through A-3 are divided; A-4 and A-5 are incomplete dorsally; A-6 and subsequent elements are complete. YPM 4 differs only in that A-4 is divided. The dorsal ends of A-1 through A-5 are fused to an inverted "V" of soft white cartilage. There is no pessulus. In each internal tympaniform membrane is a large hemispherical capsule of yellow fat, lying on a thin disc of cartilage. The diameter of the capsule is about half that of the trachea.

Stigmatura is unlike all of the above. A-1 and A-2 are divided; A-3 through A-6 are incomplete dorsally; A-7 and subsequent elements are complete. A-7 and A-8 are fused for 60° to the right of the dorsal midline. The pessulus is fused to the posterior edge of A-7 and extends posteriad, bending ventrad at the level of A-4. Its ventral end touches A-3 but is free. A thin sheet of white cartilage connects the pessulus with the dorsal ends of A-2 through A-6. The internal cartilages are extensions of this sheet, terminating at the level of B-1. A-7 through A-10 have thickenings at the dorsal midline in line with the pessulus.

Musculature.

In *Serpophaga* the Mm. tracheolaterales converge ventrally at the level of A-19 and cover the ventral two-thirds of the trachea to their insertion, on A-3 ventrally, on A-4 ventrilaterally and on A-5 laterally. M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis, directly on A-11 through A-16. M. obliquus ventralis originates immediately posterior to the insertion of M. tracheolateralis, on A-3, A-4, and A-5. It extends posterodorsally to insert along a narrow area in the middle of the A-1/B-1 membrane and on B-1, near the dorsal end.

Mecocerculus is like *Serpophaga*, differing as follows. M. tracheolateralis inserts on A-4 only. M. sternotrachealis inserts on A-11 through A-14. M. obliquus ventralis originates on A-4 only, and the direction of its fibers is posteriad. It inserts broadly in the center of the A-1/B-1 membrane.

Spizitornis is like *Serpophaga*, differing as follows. The Mm. tracheolaterales are separated ventrally by about 15° of tracheal circumference, except at their insertion on A-4, where they converge ventrally. M. sternotrachealis inserts on A-9 through A-12. M. obliquus ventralis originates on the ventral two-thirds of A-4 and extends posteriad to insert on the A-1/B-1 membrane very close to A-1.

Inezia is unlike all of the above. The Mm. tracheolaterales converge ventrally at about A-40. Near their insertion they form a single thick mass of fibers covering the ventral third of the trachea. They insert ventrally on A-2. M. sternotrachealis divides into two fasciculi near its insertion, the dorsal one inserting directly on A-10 and A-11, adjacent to the dorsal edge of M. tracheolateralis, the ventral one inserting on the membranous sheath of M. tracheolateralis. M. obliquus ventralis originates on a common median raphe which extends between the Mm. tracheolaterales to attach to A-4 and A-5. The insertion is on the dorsal third of B-1 by a broad thin tendon.

Stigmatura is like *Inezia,* differing as follows. M. tracheolateralis inserts on A-3. M. sternotrachealis inserts on A-19 through A-26. The raphe of M. obliquus ventralis attaches to A-3 and A-4 and the muscle inserts in the center of the A-1/B-1 membrane.

Colorhamphus is unlike all of the above. The Mm. tracheolaterales converge ventrally at A-36, becoming very thin. They become narrower and thicker as one muscle posteriorly and insert in a small midventral area of A-3. M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis on A-11 and A-12. M. obliquus ventralis originates on A-2 near the ventral midline, and on A-3 just lateral to the insertion of M. tracheolateralis, extending posterolaterad to insert on the center of B-1.

Tachuris (Pls. 13 and 14) is unlike all of the above. The Mm. tracheolaterales converge ventrally at A-29 and remain in contact to their insertion. The ventral half of each muscle inserts ventrally on A-9 and A-10 (except in YPM 4, in which the insertion is on A-10 and A-11). The dorsal half inserts directly on the middle of B-1. M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis, on A-11 through A-17. M. obliquus ventralis originates on the ventral surfaces of A-8 and A-9 (on A-9 and A-10 in YPM 4) and extends posteriad parallel to and in contact with the dorsal fasciculus of M. tracheolateralis. It inserts on B-1 ventrally adjacent to the insertion of the latter muscle.

SUBFAMILY ELAENIINAE.

Specimens Examined.

Of 62 species in 16 genera, I have examined the following 33 individuals of 23 species in 12 genera:

Elaenia flavogaster (Thunberg)
Elaenia martinica (Linnaeus)
Elaenia albiceps (Lafr. and D'Orb.)
Elaenia chiriquensis (Lawrence), three specimens
Elaenia obscura (Lafr. and D'Orb.)
Elaenia fallax Sclater, two specimens
Elaenia gaimardi (D'Orbigny)
Elaenia viridicata (Vieillot)
Elaenia caniceps (Swainson)
Suiriri suiriri (Vieillot)
Suiriri affinis (Burmeister)
Sublegatus modestus (Wied)
Phaeomyias murina (Spix), two specimens
Camptostoma obsoletum (Temminck)
Camptostoma imberbe Sclater
Tyranniscus chrysops (Sclater), two specimens
Tyranniscus nigrocapillus (Lafresnaye)
Phyllomyias fasciatus (Thunberg)
Tyrannulus elatus (Latham)
Microtriccus semiflavus (Scl. and Salv.), two specimens
Leptopogon (species unknown), three specimens
Mionectes olivaceus Lawrence
Pipromorpha oleaginea (Lichtenstein), three specimens

I know of only the following descriptions by a previous author:

Elaenia flavogaster (Thunberg) — Müller (1847, p. 34; Pl. 3, figs. 11-13; 1878, p. 28)
Sublegatus modestus (Wied) — Müller (1847, p. 34; Pl. 3, figs. 16-18; 1878, p. 28)

Cartilaginous Elements.

Elaenia (Pls. 13 and 14) is typical of a number of genera. In *E. caniceps* A-1 is divided; A-2 and subsequent elements are complete. A-2 through A-4 are fused for their ventral halves and mid-dorsally, forming a rigid drum. The pessulus, which is about the same width as the A-elements, is fused to A-2 at both ends. The internal cartilages are narrow bars attached anteriorly to A-2 and curved dorsad at the posterior ends. One specimen of *E. chiriquensis* (YPM 2021), *E. flavogaster, E. martinica, E. obscura, E. gaimardi*, and *E. viridicta* differ from *E. caniceps* in that A-2 is divided and free and the drum is composed of A-3 through A-5 wholly fused. In *E. fallax* the drum consists of A-3 and A-4. In *E. albiceps* and in two individuals of *E. chiriquensis* it consists of A-3 through A-6. Except in *E. caniceps* the internal cartilages are fused to A-2 and A-3. In all species except *E. chiriquensis* and *E. martinica* the posterior third of each internal cartilage extends ventrad in a thin semicircular sheet.

Müller's brief description of *E. flavogaster* mentioned only the lack of double elements and the presence of internal cartilages.

Suiriri is like *Elaenia caniceps*, differing as follows. A-2 is divided. In *S. affinis* the internal cartilages are tear-shaped plates connected to the dorsal ends of A-2 by narrow strips. In *S. suiriri* they are short broad "J's" with the free ends directed ventrad and the other ends attached as in *S. affinis*.

Phaeomyias is like *Elaenia caniceps,* differing as follows. In YPM 2038 the drum consists of A-2 and A-3, both of which are complete. In YPM 2046 there is no drum. A-2L is divided; A-2R and A-3 are double and A-2R and A-3R are fused ventrally and medially. The medial sections of A-3 are fused to the pessulus, which extends anterodorsally to join A-4 at the dorsal midline. In both individuals the internal cartilages are narrow, tapering posterior projections of thin sheets of soft cartilage which join the dorsal ends of A-1 and A-2.

Camptostoma is like *Elaenia caniceps*, differing as follows. The drum is completely fused and is deeply indented at the dorsal midline of A-2. The internal cartilages are short straight bars anteriorly fused to A-2 and bearing flat semicircular ventral extensions, like those of *Elaenia.*

Tyrannulus is like *Elaenia caniceps,* differing as follows. A-2 is fused to A-3 at the dorsal end only; A-3 and A-4 are fused for their ventral halves and at the dorsal midline. There are two pairs of internal cartilages. The dorsal pair are narrow, tapered bars fused anteriorly to A-2 and extending to the level of B-2. The ventral pair consists of circular discs fused to the ventral ends of A-1 and to the pessulus.

Microtriccus is like *Elaenia caniceps,* differing as follows. The drum consists of A-2 through A-5, completely fused. The pessulus is fused ventrally to A-2 and is closely fitted dorsally to the drum, but not fused. An extra divided component, A-6aR, is fused to A-6 at both ends. The internal cartilages are short narrow bars, slightly curved ventrad and fused anteriorly to A-2. Their ventral edges have flat semicircular extensions, similar to those of *Elaenia.*

Phyllomyias is unlike all of the above. A-1 is divided; A-2 is double; A-3 is divided; A-4 is incomplete ventrally; A-5 and subsequent elements are complete. The dorsal ends of A-3 extend ventrad parallel to the medial portions of A-2, about halfway to the ventral surface. A short narrow pessulus is fused dorsally to A-4 and extends ventrad about two-thirds of the distance to the ventral ends of that element. The internal cartilages are broad, thin plates fused anteriorly to A-2 and extending posteriad to the level of B-2.

Sublegatus is like *Phyllomyias,* as nearly as can be determined from the specimen at hand, in which the dorsal region from B-1 through A-3 is severely shot damaged. Müller's brief description of *Sublegatus* stated only that there is one double element and large internal cartilages.

Tyranniscus is unlike all of the above. In *T. chrysops* A-1 is divided; A-2 is double; A-3 is divided; A-4 is incomplete dorsally; A-5 and subsequent elements are complete. In YPM 922 A-5 and A-6 are fused; in YPM 2010 the left halves of A-4 and A-5 are fused and the dorsal end of A-3R is fused to A-2R. The pessulus is fused ventrally to A-4 and extends dorsally and anteriorly to A-5, to which it is also fused. In YPM 2010 the fusion also includes the left dorsal end of A-4. The internal cartilages are straight narrow plates fused to the dorsal end of A-2 and extending posteriad to the level of B-4. A narrow strip of cartilage joins the ventral ends of B-1 and B-2. *T. nigrocapillus* differs from *T. chrysops* in having A-2 divided; A-4 complete and wholly fused to A-5; the internal cartilages shorter, extending only to B-1 and bearing a ventrally directed fin; and B-1 not connected to B-2.

Leptopogon is unlike all of the above. A-1 and A-2 are divided; A-3 is incomplete dorsally; A-4 and subsequent elements are complete, except in AMNH 819, in which A-4 is incomplete dorsally and subsequent elements complete. The pessulus is free ventrally in all three individuals and is free dorsally in AMNH 820 and 821. In AMNH 819 it is continuous with the dorsal end of A-4. The internal cartilages are narrow (about half the width of the A-elements) and extremely thin. They extend from their attachment at A-2 to the level of B-4.

Pipromorpha (Pls. 13 and 14) is unlike all of the above. A-1 is divided; A-2 is double; A-3 and subsequent elements are complete. A-2 through A-6 are fused so completely that seams remain only laterally. The pessulus is an integral part of the drum, fused dorsally and ventrally to A-3 and medially to A-2, where lines of fusion are still visible. Each of the internal cartilages is a long blade extending posteriad from a flattened ball, which, in turn, is connected to A-2 by a narrow curved "stalk." The stalk comprises about one-third the total length of the cartilage, which extends posteriad to the level of B-7. The B-elements are all divided and differ from those of the above genera in that B-3 is the largest. The first three elements are enlarged at their ends; the remaining ones are unmodified.

Mionectes is like *Pipromorpha*, differing only in the form of the internal cartilages. They are identical in outline to those of *Pipromorpha*, but lack the ball at the anterior end of the blade.

Musculature.

In *Elaenia* (Pls. 13 and 14) there is considerable variation in the position of the Mm. tracheolaterales. In most species there is a midventral space of 15 to 45° of circumference, the widest being in *E. gaimardi*. In *E. chiriquensis* the pair are in contact from A-11 to their insertion and in *E. martinica*, *E. fallax*, *E. viridicata* and *E. caniceps* from about A-25 to their insertion. In all species the insertion is mostly on the anterior edge of the drum, the precise area being variable. In *E. chiriquensis* and *E. obscura* the ventral and lateral fibers attach to the anterior edge of the drum, while the middle part of the muscle extends to the ventrilateral surface of A-3. In all of the other species the ventral fibers extend further posteriad, to A-3 or A-2 and the insertion as a whole forms a spiral line to the lateral anterior edge of the drum.

M. sternotrachealis inserts directly on A-9 and A-10 in *E. flavogaster*, on A-10 through A-12 in *E. martinica*, on A-15 through A-19 in *E. albiceps*, on A-17 through A-24 in *E. chiriquensis*, on A-14 through A-17 in *E. obscura* and *E. fallax*, and on A-14 through A-16 in *E. caniceps*. In *E. gaimardi* the dorsal half of the fibers inserts directly on A-13 through A-17 at the dorsal edge of M. tracheolateralis, while the ventral fibers are continuous with those of the latter. In *E. viridicata* there are three fasciculi: the posterior dorsal third of the fibers insert directly on A-13 and A-14; the anterior dorsal third are continuous with M. tracheolateralis; the ventral third insert on the midventral surface of the membranous sheath surrounding M. tracheolateralis.

The intrinsic musculature of *Elaenia caniceps* is typical of a number of species. M. obliquus ventralis originates on a raphe attached to the ventral midline of the drum and inserts by a broad tendon to the dorsal third of B-1. M. obliquus lateralis originates directly on the dorsolateral surfaces of A-4 and A-5 and along a line from there to the ventrilateral surface of A-2. It inserts directly on the middle third of A-1. *E. viridicata* differs from *E. caniceps* only in that the tendon of M. obliquus ventralis is very narrow. In *E. albiceps* the raphe of M. obliquus ventralis is attached to A-5 through A-7 and the muscle inserts on the A-1/B-1 membrane, near the middle of A-1. In *E. flavogaster, E. martinica, E. fallax*, and *E. gaimardi* the insertion is on the posterior edge of A-1. In *E. chiriquensis* and *E. obscura* the ventral muscle originates directly on the drum, adjacent to the ventral midline and ventrilaterally on A-5 and A-4, and inserts directly on the ventral third of A-1. M. obliquus lateralis originates on the lateral surfaces of A-5 and A-4 and inserts on A-1, dorsally adjacent to the insertion of M. obliquus ventralis. The origins of the two muscles are separated by the ventrilateral extension of M. tracheolateralis, except in one specimen of *E. chiriquensis*, in which the origins are continuous through a very narrow connecting region. Müller found M. obliquus ventralis inserting on A-1 in *E. flavogaster* but did not mention a second intrinsic muscle.

Camptostoma is like *Elaenia caniceps*, differing as follows. M. sternotrachealis inserts on A-10 and A-11. M. obliquus lateralis inserts on the middle of B-1 by a broad tendon extending beneath that of M. obliquus ventralis.

Suiriri is like *Elaenia caniceps*, differing as follows. The Mm. tracheolaterales are separated ventrally by about 20° of tracheal circumference. M. sternotrachealis inserts directly on A-11 through A-15, partly beneath the dorsal edge of M. tracheolateralis. In *S. affinis* the tendon and insertion of M. obliquus ventralis are broader than in *E. caniceps*, covering the dorsal half of B-1.

Phaeomyias is like *Elaenia caniceps*, differing as follows. The Mm. tracheolaterales are separated ventrally by about 15° of tracheal circumference. They insert on A-2 ventrally, on A-3 ventrilaterally, and on A-4 and A-5 laterally. M. sternotrachealis inserts on A-9 through A-13. The raphe of M. obliquus ventralis is attached to A-2 through A-4. The muscle inserts by a broad tendon in YPM 2046 but by a very narrow one in YPM 2038. M. obliquus lateralis originates on A-3 and A-4 ventrilaterally and on A-4 and A-5 laterally. In YPM 2046 the insertion is as in *Elaenia*, while in YPM 2038 some dorsal fibers of M. obliquus lateralis are attached to the tendon of M. obliquus ventralis.

Tyrannulus is like *Elaenia obscura*, differing as follows. M. tracheolateralis inserts on A-4 only, and M. sternotrachealis on A-11 through A-14. M. obliquus ventralis originates near the ventral midline of A-2 and A-3 as well as ventrilaterally and laterally on A-3 and A-4. It inserts in the center of the A-1/B-1 membrane. An M. obliquus lateralis is not separable from the ventral muscle, although the deep dorsal fibers are more anteroposteriorly oriented than the superficial ones.

Microtriccus is unlike all of the above. The Mm. tracheolaterales converge ventrally at about A-30 (variable) and cover the ventral half of the trachea from there to their insertion on A-5 ventrally and A-4 laterally. M. sternotrachealis inserts directly on the lateral surfaces of A-9 through A-12. M. obliquus ventralis originates directly on the drum, near the ventral midline of A-3 through A-5, and inserts in a small area near the dorsal end of B-1. M. obliquus lateralis is lacking.

The two species of *Tyranniscus* examined differ strongly from each other. *T. nigrocapillus* is like *Microtriccus*, differing as follows. M. tracheolateralis inserts on the entire ventral half of A-2. M. sternotrachealis inserts on A-11 through A-13. M. obliquus ventralis originates on a raphe attached midventrally to A-3 through A-5. It extends superficial to M. tracheolateralis to insert directly on B-1, near the dorsal end.

In *Tyranniscus chrysops* the Mm. tracheolaterales converge at A-33 and diverge again at the level of A-6. Each inserts directly in the center of the respective A-1/B-1 membrane. M. sternotrachealis inserts directly on the lateral surfaces of A-13 through A-18. There are no intrinsic muscles.

Leptopogon is unlike all of the above. The Mm. tracheolaterales converge ventrally, becoming narrower and thicker as one muscle and terminating in a blunt point at A-4. They insert by a pair of narrow tendons passing the raphe of the Mm. obliqui ventrales and attaching to the ventral ends of A-1 and B-1. At the level of A-2 the pair of tendons are connected by a short vinculum. The Mm. sternotracheales are variable among the three specimens. In AMNH 819 they insert directly on the lateral surfaces of A-5 through A-7; in AMNH 821 the ventral half of each muscle is continuous with M. tracheolateralis; in AMNH 820 the right M. sternotrachealis is wholly continuous with M. tracheolateralis, while the left inserts directly. M. obliquus ventralis originates on a raphe attached to the ventral midline of A-2 and A-3 and inserts near the dorsal end of B-1.

Phyllomyias is unlike all of the above. The Mm. tracheolaterales converge ventrally at the level of A-27. At A-4 each muscle divides into two fasciculi, a large ventral one inserting on A-3 and a small lateral one inserting on A-2. M. sternotrachealis also divides into two fasciculi. The dorsal branch inserts directly on the lateral surfaces of A-10 through A-16 and the ventral one on the membranous sheath surrounding M. tracheolateralis. M. obliquus ventralis originates on A-2 and A-3 near the ventral midline and extends laterad to insert near the center of the A-1/B-1 membrane.

Sublegatus is like *Phyllomyias*, but from the damaged specimen on hand one can only determine that M. sternotrachealis inserts as above and that M. tracheolateralis does not branch near its insertion. Müller mentioned only that M. obliquus ventralis inserted on B-1, and that the dorsal ["hintere," translated by Bell (Müller, 1878) as "posterior"] section of the syrinx is free of muscle.

Pipromorpha (Pls. 13 and 14) is unlike all of the above. The Mm. tracheolaterales converge ventrally at the level of A-37 and become narrower and thicker until, at their insertion on A-6, their combined width is about 30° of tracheal circumference. The majority of the resultant midventral muscle appears to consist of the left muscle. M. sternotrachealis inserts directly on the ventrilateral surfaces of A-11 through A-13. M. obliquus ventralis originates on A-6 immediately posterior to the insertion of M. tracheolateralis and extends posteriad to insert on the ventral quarter of A-1 and, by a short tendon, on B-1.

Mionectes is like *Pipromorpha,* differing as follows. M. sternotrachealis is about twice as thick as that of *Pipromorpha*, its diameter being about one-third that of the trachea. The anterodorsal third of the muscle is continuous with M. tracheolateralis; the posterodorsal third inserts directly on A-7 through A-10; the ventral third inserts on the membrane surrounding M. tracheolateralis. The insertion of M. obliquus ventralis is by a broad tendon to B-1.

FAMILY OXYRUNCIDAE. SHARPBILL.

Specimens Examined.

I have examined one specimen of *Oxyruncus cristatus* (Gmelin), the only species in this family. The only previous description of the syrinx is that by Clark (1913, p.403), who noted only that the syrinx of *Oxyruncus* bore "a striking resemblance to *Sayornis* and *Tyrannus*." He commented further that "the tongue and syrinx are so much like those of *Sayornis* that the only difference noted is that the tongue is a little more horny than in the Phoebe."

Cartilaginous Elements.

A-1 is a broad, divided element; A-2 is narrow, about half the width of A-1, and double; A-3, also narrow, appears to be divided, but has a long dorsomedial section; A-4 is wide and incomplete ventrally; A-5 and subsequent A-elements are complete. All of the B-elements are divided. A thick, narrow, slightly curved pair of internal cartilages is fused to A-2 and extends posteriad to the level of B-2. A narrow pessulus is fused dorsally and ventrally to A-4, which is indented where it meets the pessulus mid-dorsally.

Musculature.

The Mm. tracheolaterales broaden at about A-40 to cover the ventral half of the trachea. They converge ventrally so that at A-10, where the Mm. sternotracheales reach the trachea, the combined Mm. tracheolaterales cover only about 60° of tracheal circumference. They continue to converge and thicken until, at their insertion near the ventral midline of A-1 and A-2 (and on the connective tissue between the elements), the combined muscle mass is only about 30° wide. There is some connective tissue between the muscle and the ventral ends of B-1, but, due to the soft condition of the specimen, I am unable to determine whether or not this tissue is tendinous. Each M. sternotrachealis is wholly continuous with the dorsal edge of the respective M. tracheolateralis which it meets at A-10.

A conspicuous pair of intrinsic muscles, for which the name Mm. obliqui ventrales appears justified, originates on the ventral ends of A-3 and A-4, covered by the Mm. tracheolaterales. The intrinsic muscles extend posterolaterally, then posterodorsally, to insert on the center of B-1.

FAMILY PHYTOTOMIDAE. PLANTCUTTERS.

Specimens Examined.

Of the three species in the single genus, I have examined the following four specimens in two species:

Phytotoma rara Molina, two specimens
Phytotoma rutila Vieillot, two specimens

I know of only the following description by a previous author:

Phytotoma rara Molina — Kuchler (1936)

Cartilaginous Elements.

The two species examined are very similar. A-1 is divided. A-2 is complete in *P. rutila* and incomplete dorsally in *P. rara* (Pls. 17 and 18). In both species the posterior edge of A-2 is extended posteriad and is fused to the ventral end of the pessulus. In *P. rutila* the dorsal side is similar to the ventral one. In *P. rara* the dorsal end of A-2L extends posteriorly between the ends of A-1 and is fused to the dorsal end of the pessulus. A-3 and subsequent elements are complete. All of the B-elements are divided and are D-shaped in cross section. Only B-1, which lies very close to A-1, is spatulate at the ends. These findings agree closely with those of Kuchler.

Musculature.

The Mm. tracheolaterales are narrow, each covering about 30° of tracheal circumference. At the insertion of M. sternotrachealis, M. tracheolateralis divides into two fasciculi, the dorsal one inserting laterally on A-12 in *P. rutila* and on A-14 in *P. rara,* the ventral one inserting on the B-1/B-2 membrane, just posterior to the center of B-1. In one specimen of *P. rutila* the ventral tenth of the fibers insert on B-1. M. sternotrachealis inserts in an oval area on the lateral surfaces of A-10 through A-12 in *P. rutila* and A-11 through A-14 in *P. rara.* Kuchler described and illustrated M. tracheolateralis as inserting on the middle of B-1, but otherwise his findings agree with the above.

FAMILY PITTIDAE. PITTAS.

Specimens Examined.

Of 23 species in a single genus, I have examined the following four individuals of four species:

Pitta reichenowi Madarasz
Pitta boschi Müller and Schlegel
Pitta erythrogaster Temminck
Pitta atricapilla Lesson

I know of only the following descriptions by previous authors:

Pitta angolensis Vieillot — Garrod (1877)
Pitta cyanura (Boddaert) — Garrod (1877)
Pitta cyanoptera Temminck — Köditz (1925)
Pitta simillima Gould — Köditz (1925)
Pitta schwaneri Bonaparte — Köditz (1925)

Cartilaginous Elements.

All of the specimens examined are basically similar. In *Pitta reichenowi* (Pls. 17, 18) A-1 and A-2 are divided: there is an extra divided element A-2aR; A-3 and A-4 are incomplete dorsally; A-5 and subsequent elements are complete. There is no pessulus. The line of juncture of the two internal tympaniform membranes is oblique, extending from A-5 dorsally to A-3 ventrally.

P. boschi is like *P. reichenowi* except that A-3 is divided. In *P. erythrogaster* A-1 through A-4 are divided; A-5 and A-6 are incomplete dorsally; and there is no unpaired element. In *P. atricapilla* A-3 is incomplete dorsally and the unpaired divided element is A-3aR. A-4 and A-5 are complete and are fused ventrally.

In *P. angolensis,* Garrod found A-1 and A-2 divided. A-3 and A-4 were incomplete dorsally and fused. Although referring to the divided A-elements as "bronchial ring-segments," he noted that they appeared "like moieties of true tracheal rings." The pessulus was lacking and there was no extra element. In *P. cyanura* Garrod found A-1 through A-4 divided and A-5 and A-6 incomplete dorsally. The illustrations accompanying Garrod's text show four A-elements on the right and only three on the left, divided or incomplete. Although possibly an error on the part of the artist, the asymmetry in the drawing may well be accurate and Garrod's count based on the right side only.

Köditz' descriptions are in agreement with those of *P. erythrogaster,* above. In *P. cyanoptera* he found a short pessulus, lacking in the other two species examined by him.

Musculature.

The syringeal musculature appears to be essentially the same in all species of *Pitta*. M. tracheolateralis is narrow and lies on the ventrilateral surface of the trachea. It inserts on the ventrilateral surface of B-1. M. sternotrachealis is variable. In *P. reichenowi* it inserts directly on A-8 through A-10, at the dorsal edge of M. tracheolateralis; in *P. boschi* it inserts on A-9 through A-14. In *P. erythrogaster* and *P. atricapilla* M. sternotrachealis is wholly continuous with M. tracheolateralis.

The descriptions by Garrod and Köditz are in close agreement with *P. erythrogaster,* above.

FAMILY PHILEPITTIDAE. ASITIES AND FALSE SUNBIRDS.

Specimens Examined.

Of four species in two genera, I have examined the following two individuals, one of each genus:

Philepitta castanea (P.S. Müller)
Neodrepanis coruscans Sharpe

I know of only the following descriptions by previous authors:

Philepitta "probably *castanea*" — Forbes (1880b)
Neodrepanis coruscans Sharpe — Amadon (1951)

The specimen of *Neodrepanis* examined by me was the same individual as was studied by Amadon.

Cartilaginous Elements.

In *Philepitta* (Pls. 17 and 18) A-1 is incomplete dorsally. The right and left halves of the element are like the components of a divided element, lying in planes about 30° from the sagittal plane and joined at their ventral ends in a sharp point. The dorsal ends of A-1 are broadly spatulate. A-2 is complete and sharply folded around the dorsoventral axis. It is fused to A-1 for its ventral half. The pessulus is fused to A-2 at both ends. The remaining A-elements are complete and all of the B-elements are divided. B-1 and B-2 are very thin, straighter than the rest, and pointed at the ventral ends. Their straightness results in a narrowing of the tubes at that point.

Forbes' detailed description of *Philepitta* agrees closely with the above. He did not find fusion of A-1 and A-2, but noted that they were "closely apposed." The lateral view of the syrinx is inverted in Forbes' figure, but otherwise his illustrations closely approximate my specimen.

Neodrepanis (Pl. 20) is like *Philepitta,* differing as follows. The dorsal ends of A-1 are fused to A-2, but the ventral ends are free. A short triangular pair of internal cartilages are fused to the dorsal ends of A-1 and A-2. B-1 and B-2 are not modified as in *Philepitta;* they are as heavy and as curved as the other B-elements. Amadon's description of *Neodrepanis* was mainly concerned with the major points of comparison of this genus with *Philepitta* and did not go into detail.

Musculature.

The syringeal muscles of both genera are very simple. In *Philepitta* M. tracheolateralis is a broad lateral band, which divides into two fasciculi at the level of A-6. The fasciculi extend on the dorsal and ventral sides, respectively, of M. sternotrachealis and insert along nearly the entire length of A-1. M. sternotrachealis inserts in a roughly circular area on the lateral surfaces of A-5 and A-6. Near the insertion the fibers fan out beneath those of M. tracheolateralis. There are no intrinsic muscles. Forbes' description of the musculature of *Philepitta* agrees closely with the above.

Neodrepanis is like *Philepitta,* differing as follows. M. tracheolateralis is narrower, situated more ventrally, and does not divide into two fasciculi. Its insertion is along the ventral half of A-1. M. sternotrachealis inserts partly in continuity with the dorsal superficial fibers of M. tracheolateralis and partly on the membrane covering the ventral surface of the latter muscle.

FAMILY ACANTHISITTIDAE. NEW ZEALAND WRENS.

Specimens Examined.

Of the four species in this small family, I have examined the following two specimens:

Acanthisitta chloris (Sparrman)
Xenicus longipes (Gmelin)

I know of only the following description by a previous author:

Xenicus longipes (Gmelin) — Forbes (1882)

Forbes also mentioned very briefly the syrinx of *Acanthisitta chloris.*

Cartilaginous Elements.

In *Acanthisitta* (Pl. 19) the A- and B-elements are not as easily distinguished as in most other suboscines. The most anterior *free* divided element, which I have designated B-1, is thicker and narrower than that immediately anterior to it. Like the elements posterior to it, B-1 consists of a thick, ossified center section, about two-thirds of the total length of the element, and a soft, thinner section on each end. The first three B-elements are about half as wide as the remaining ones.

A-1 through A-4 are fused into a solid drum that bulges prominently in the lower ventral region and is indented at the ventral midline. A-1 is a divided element; A-2 is incomplete dorsally; A-3 and subsequent elements are complete. The seams between the fused elements are visible laterally and dorsally. The pessulus is firmly fused to the drum ventrally, where it is quite narrow. At its dorsal end the pessulus broadens and bends anteriad, forming a plate closely fitted between the ends of A-2 and just reaching A-3. Due to the age of the specimen, I was unable to determine whether or not the pessulus was fused to A-2R, as it was to A-2L.

Lying in the internal tympaniform membranes between the pessulus and the dorsal ends of B-4 is a pair of straight, narrow internal cartilages. At their anterior ends these cartilages are very close to, possibly even attached to, the pessulus.

Xenicus is almost identical to *Acanthisitta* in its syringeal cartilages, differing in having a drum of three elements (A-1 through A-3) and in lacking internal cartilages. Forbes' description and illustration of the syrinx of *Xenicus* agree closely with my specimen. He noted the close similarity of *Acanthisitta* to *Xenicus,* but did not mention internal cartilages.

Musculature.

In *Acanthisitta* the Mm. tracheolaterales are narrow for their entire length. Those fibers not continuous with the Mm. sternotracheales insert on the ventrilateral surfaces of A-2 through A-5. The posterior part of this pair of muscles is enclosed in a membranous sheath that becomes increasingly fibrous and silvery in color posteriorly, in the region between the muscles. The sheath ends at the level of A-3 and is lightly attached to the drum at that point. Laterally the sheath seems to be less aponeurotic. M. sternotrachealis inserts directly on the lateral surfaces of A-7, A-8 and A-9, with some anterior fibers continuous with those of M. tracheolateralis. There are no intrinsic muscles.

Xenicus is closely similar to *Acanthisitta,* differing only in that M. tracheolateralis inserts on A-6 and A-7, as well as in continuity with M. sternotrachealis. The latter, in addition to this continuity, inserts directly on A-5, A-6 and A-7. The sheath surrounding the lower trachea is more fibrous than in *Acanthisitta* and encloses both pairs of muscles down to the level of A-8.

Forbes' description of the syringeal muscles was concerned mainly with the absence of intrinsic muscles. He noted that in *Xenicus* there was a "thin lateral muscle terminating on the upper edge of the drum," presumably on A-3. The accompanying illustration, however, shows the muscle as terminating on the third or fourth element anterior to the drum, as it does in my specimen.

SUBORDER MENURAE

FAMILY MENURIDAE. LYREBIRDS.

Specimens Examined.

Of two species in the single genus, I have examined only the following individual:

Menura novae-hollandiae Latham (nestling)[1]

I know of only the following descriptions by previous authors:

Menura novae-hollandiae Latham — Eyton (1841b)
Menura novae-hollandiae Latham — Garrod (1876)

Cartilaginous Elements (see Pls. 17 and 18).

A-1, A-2 and A-3 are divided and are straighter than other A- or B-elements. A-1, the least curved, is narrow ventrally and broad dorsally, where it has a terminal posteriad projection. A-2, slightly more curved, is widest at the ventral end, where its width is about twice that of the dorsal end. A-3 is much narrower than the other two, more strongly curved around the tracheal axis, and fitted to A-4 but not fused. A-4 is complete and is bent at the dorsoventral axis. The pessulus is fused to A-4 at both ends. A-5 and subsequent elements are complete and similar to each other. Garrod reported the lower 16 complete elements to be anteroposteriorly compressed, describing them as "carinate . . . compressed from above downward." My specimen shows no such condition, but it is possible that the elements are modified as the individual matures.

A thick, fibrous syringeal aponeurosis extends from the esophagus, to which it is attached, to the trachea. It is attached to elements A-14 through A-24 and is continuous ventrally with the anterior wall of the interclavicular air sac. The aponeurosis is broad posteriorly but very narrow (about one-tenth of the tracheal diameter) in the region of A-3 through A-10. In this region it lies against the trachea in a slot between the Mm. bronchiales postici.

Musculature.

M. tracheolateralis extends down each side of the trachea to insert on the syringeal aponeurosis and on the lateral and dorsolateral surfaces of A-20 (dorsolaterally) through A-25 (laterally). M. sternotrachealis originates on the internal costal processes of the sternum and inserts on the lateral surfaces of A-6 through A-9.

There are three pairs of intrinsic muscles, which correspond closely to certain of the intrinsic muscles of the oscines. The names applied to the oscine muscles are therefore used here (see page 89).

M. bronchotrachealis anticus originates on the ventrilateral surfaces of A-24 and A-25 and on the posterior surface of the syringeal aponeurosis. It extends posteroventrad to insert subterminally on the ventral end of A-2.

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[1] Through the kindness of the Trustees of the Australian Museum, Sydney, I have examined the syrinx of an adult female *Menura novae-hollandiae* (one of two specimens in the collection of the Carnegie Museum). The syrinx of the adult differs from that of the nestling only in size. (Footnote added in galley proof.)

M. bronchotrachealis posticus originates on the dorsolateral surface of A-22 through A-24. It extends posteriad to insert on the dorsal end of A-1.

M. bronchialis posticus originates in a broad area on the dorsal and dorsolateral surfaces of A-14 through A-18 and on the posterior surface of the syringeal aponeurosis, near the dorsal midline. Its region of origin is anterolaterally continuous with that of M. bronchotrachealis posticus. M. bronchialis posticus inserts on the dorsal ends of A-2, A-3, and A-4.

The above description is in close agreement with Garrod's, differing only slightly in the insertions of the extrinsic muscles and the origins of the intrinsic muscles. Eyton's description is similar, except that M. bronchialis posticus has been omitted.

FAMILY ATRICHORNITHIDAE, SCRUB-BIRDS.

Specimens Examined.

Of the two species in this small Australian family I have examined the following:

Atrichornis clamosus (Gould)

The only previous description of the syrinx in this family appears to be the following, devoted to the other species:

Atrichornis rufescens (Ramsay) — Garrod (1876)

Cartilaginous Elements.

There are three heavy, divided A-elements, A-1 through A-3 (see Pl. 19). All are strongly curved around the tracheal axis. A-1, the heaviest of the three, has a robust posteriad extension at the dorsal end. A-2 is about twice as wide near the ventral end as at the dorsal end. There is a prominent ridge at the posterior edge of the ventral third of the element. A-3 is about the same width as A-2 at the dorsal end and tapers to a rounded point at the ventral end. A-4 is complete and extends posteriad midventrally to carry the pessulus, which is also fused to it mid-dorsally. A-4 and A-5 are fused mid-dorsally and are closely attached together by stiff connective tissue along their entire region of contact.

Garrod's description of *A. rufescens* mentions only that it "presents precisely the same arrangement as *Menura*." He noted the dorsal posteriad extension of A-1 and the ventral widening of A-2. These points do not show well in his illustration, but we may infer from his text that *A. rufescens* is similar to *A. clamosus* in its syringeal cartilages.

Musculature.

The Mm. tracheolaterales widen dorsally until at their insertion they cover the entire dorsal two-thirds of the trachea with a thin sheet of muscle which is somewhat thicker at its ventral edge. The insertion is on the anterior surface of the syringeal aponeurosis and on the underlying elements, A-13 through A-17.

M. sternotrachealis originates on the lateral edge of the internal surface of the coracoid process of the sternum and inserts on the lateral surfaces of A-4 and A-5.

There are three well-developed pairs of intrinsic muscles, the positions of which correspond so well to those of certain muscles of the oscine syrinx that the use of the same names appears warranted. (For a description of the oscine muscles, their nomenclature and synonymy, see p. 89). M. bronchotrachealis anticus originates ventrally and ventrilaterally on the aponeurosis, ventrilaterally on A-13 through A-16, and, along its medial edge from A-4 (where the members of the pair are almost in contact), through A-16. The medial fibers of this muscle are short and occupy essentially the same position as does M. bronchialis anticus pars medialis in most oscines. In *Atrichornis,* however, there is complete continuity of origin and of insertion in this muscle mass, so the naming of the short medial fibers as a separate muscle does not seem warranted.

M. bronchotrachealis posticus originates on the posterior surface of the aponeurosis and on adjacent areas of A-12 dorsally through A-15 laterally. It inserts on the dorsal ends of A-3 and A-4. The muscles of this pair are in contact at the dorsal midline from origin to insertion.

A long, substantial M. bronchialis posticus lies posteroventral to M. bronchotrachealis posticus, originating on the ventrilateral surfaces of A-5 through A-9 and inserting on the dorsal ends of A-1 and A-2 and on the connective tissue between them.

The above differs substantially from the description by Garrod that has served for nearly a century as the basis for the belief that *Atrichornis* possesses only two pairs of intrinsic muscles. He described a long dorsal muscle originating on the aponeurosis and inserting on the dorsal end of A-1. He also noted the presence of the long ventral muscle but did not mention any fibers originating along the medial edge. Garrod did not find any muscle to correspond to M. bronchialis posticus, but it might have been overlooked due to poor preservation or inadequate magnification. In his illustration there is clearly a space in the region occupied in *A. clamosus* by M. bronchialis posticus.

SUBORDER PASSERES ("OSCINES")

NOMENCLATURE.

The nomenclature employed for the previous suborders is used for the oscines, with the following modifications.

Cartilaginous Elements (Pl. 21).

The oscine syrinx is characterized by the presence of a drum formed by the fusion of three or four complete elements. Posterior to the drum are three divided elements often known as "intermediary bars" (Owen, 1866) or "bronchial bars" (most other European authors). These elements are heavy and bony, round or slightly flattened in section, and concave posteriorly or straight. Posterior to them are other divided elements which are slender, wholly or partly cartilaginous, round or D-shaped in section, and slightly concave anteriorly.

The interrelationships of the oscine syringeal elements have always been controversial and at least four different nomenclatures have been used (Table 3). MacGillivray (1839) considered the "intermediary bars" to be tracheal elements, numbering them anteriad in continuity with the drum (which he considered a single element) and other complete elements. Owen (1866) treated the "bars" as neither tracheal nor bronchial, numbering them anterior to posterior. He numbered the "tracheal rings" anteriad from the element nearest the drum, leaving the latter unnumbered. Elements posterior to the "intermediary bars" were designated "bronchial semirings" and numbered from anterior to posterior. Wunderlich (1886), in a system followed by most subsequent European authors, treated all divided elements as "bronchial bars" or "semirings," numbering them posteriad from the one closest to the drum. Complete elements were numbered anteriad, starting with the one anterior to the drum. Miskimen (1951) followed Owen's system, except that she reversed the numbering of the intermediary bars.

TABLE 3. Synonymy of syringeal cartilages in the suborder Passeres.

Ames, modified from MacGillivray, 1839	Owen (1866)[1]	Miskimen (1951)[2]	Wunderlich (1886)[3]
A-9	Tracheal ring II	Tracheal ring II	Tracheal ring II
A-8	Tracheal ring I	Tracheal ring I	Tracheal ring I
A-7 A-6 A-5 A-4 } Drum	Drum	Drum	Drum ("Trommel")
A-3	Intermediary Bar I	Intermediary Bar III	Bronchial Bar I
A-2	Intermediary Bar II	Intermediary Bar II	Bronchial Bar II
A-1	Intermediary Bar III	Intermediary Bar I	Bronchial Bar III
A-1/B-1 Membrane	External tympaniform membrane		
B-1	Bronchial semiring I	Bronchial semiring I	Bronchial semiring IV
B-2	Bronchial semiring II	Bronchial semiring II	Bronchial semiring V
B-3	Bronchial semiring III	Bronchial semiring III	Bronchial semiring VI

[1] This method was also used by Shufeldt (1890).
[2] This method was also used by Berger (1957).
[3] This method was also used by Fürbringer (1888), Gadow and Selenka (1893), Haecker (1900), Setterwall (1901) and Köditz (1925).

Precise evolutionary or developmental homology between the "intermediary bars" of the oscines and the lower A-elements of other suborders is difficult to confirm, but there is much to suggest a close relationship. The shape and composition of the bars correspond to those of A-elements, while the configuration of the divided elements posterior to the bars is more like that of the B-elements. Moreover, the bars are closely fitted to each other and the most anterior of them lies in a groove in the edge of the drum. Authors who have considered the bars as part of a bronchial series have also recognized the disjunct nature of the series in naming the membrane between the posterior bar and the next posterior element, the Membrana tympaniformis externa.

In the following descriptions I utilize the concept held by MacGillivray (1839) that the "intermediary bars" and the drum are part of a natural series continuous with the anterior complete elements. The similarity of this series to those of many members of other suborders urges the use of the "A" and "B" designations employed elsewhere. Among the large variety of syringeal patterns in the Tyranni are several that closely approach the oscine configuration structurally, the closest that I have examined being that of *Elaenia chiriquensis*.

Musculature.

The intrinsic syringeal muscles of the Passeres have been described with more than a dozen systems of nomenclature (Table 4). Conceptural differences regarding what constitutes a single muscle have led to various figures for the total number of oscine muscles. The disagreement centers upon two questions: 1) whether muscles should be named on the basis of function or of location, and 2) whether a single mass of muscle fibers attached to several cartilaginous elements constitutes one muscle or several. My choice of Owen's (1866) nomenclature is based on its applicability to a large number of oscine syringeal patterns, rather than on concepts.

Savart (1826) named four pairs of muscles in *Corvus* on the basis of their action on individual cartilages. His system was not used by any subsequent author. Owen (1866) provided the simplest of the several nomenclatures used by recent authors, recognizing five pairs of intrinsic muscles. In an unfortunate attempt to homologize the axes of the avian body with those of man he named ventral muscles "anticus" and dorsal ones "posticus." Wunderlich (1886) named seven pairs of muscles on a functional basis. Using the positions of the muscles, Fürbringer (1888) named eight pairs, to which Mayr (1931) added a ninth. Setterwall (1901), basing his system on muscle positions, produced a wholly different nomenclature, also with eight muscles. Köditz (1925) combined the systems of Fürbringer and Setterwall, recognizing eight pairs of muscles, one of which is not synonymous with any of those named by his predecessors. Köditz was the only author whose nomenclature was not based on a corvid (*Corvus* or *Pica*), hence the difference in application.

With the exception of Owen's, each of the above systems requires the addition of many new names to be applicable to all the oscines. Until more is known about the operation of the syrinx it seems unwise to name the muscles on a functional basis or to employ functional groupings of muscle fasciculi. I have modified Owen's nomenclature by the merger of two dorsal muscles and the recognition of two parts to one of the ventral muscles, resulting in the following system.

The extrinsic muscles are the same as in the other suborders: M. tracheolateralis and M. sternotrachealis.

The following four pairs of intrinsic muscles are recognized:

1) M. bronchotrachealis posticus originates dorsally and dorsolaterally on the syringeal aponeurosis and on the elements immediately posterior to the attachment of the aponeurosis. It extends posteriad to insert on the dorsal ends of A-1, A-2, and/or sometimes A-3, with some fibers attached to the connective tissue between the elements. The medial portion of M. bronchotrachealis posticus was treated by Owen as M. bronchotrachealis brevis, but in view of the frequent continuity of origin and insertion the two are best treated as one muscle.

2) M. bronchotrachealis anticus is the ventral counterpart of M. bronchotrachealis posticus, originating ventrilaterally on the syringeal aponeurosis and on the elements posterior to it, and extending posteriad to insert on the ventral end of A-1 and/or A-2.

3) M. bronchialis posticus is a short deep muscle on the dorsolateral surface of the syrinx, originating on the lateral surface of the drum and/or on the elements immediately anterior to the drum. It extends posterodorsally to insert on the dorsal end of A-1 (sometimes also on A-2) immediately ventral to the insertion of M. bronchotrachealis posticus.

TABLE 4. Synonymy of syringeal muscles in the suborder Passeres.

Owen (1866) Shufeldt (1890) Miskimen (1951) Ames, modified.	Wunderlich (1886)	Gadow and Selenka (1893) Fürbringer (1888) Haecker (1900)	Setterwall (1901)	Köditz (1925)
Corvus corax or *brachyrhynchos*	*Pica pica*	*Corvus corone*	*Pica pica*	*Pycnonotus, Irena.*
M. broncho-trachealis anticus	M. levator longus anterior arcus secondi	M. tracheo-bronchialis ventralis	M. ventralis longus	M. laryngo-syringeus ventralis (longus)
M. broncho-trachealis posticus	M. levator longus posterior arcus secondi	M. tracheo-bronchialis dorsalis longus	M. dorsolateralis longus	M. laryngo-syringeus dorsolateralis
M. broncho-trachealis brevis. (I do not feel that this muscle is separable from the preceding.)	M. tensor membranae tympaniformis internae	M. tracheo-bronchialis dorsalis brevis	M. dorsalis longus	M. laryngo-syringeus dorsalis
		M. syringeus dorsalis	M. dorsalis brevis	M. syringeus dorsalis (brevis)
M. bronchialis posticus	M. levator brevis posterior arcus secondi	M. syringeus dorsolateralis	M. dorsolateralis brevis	M. syringeus dorsolateralis (brevis)
		M. interbronchialis lateralis (Mayr, 1931)		
M. bronchialis anticus, pars medialis	M. rotator arcus tertii	M. tracheo-bronchialis obliquus	M. ventrilateralis brevis externus	M. laryngo-syringeus ventrilateralis (longus)
pars lateralis	M. levator brevis anterior arcus secondi	M. syringeus ventralis	M. ventralis brevis	M. syringeus ventrilateralis externus (brevis externus)
	M. laxator membranae tympaniformis externa	M. syringeus ventrilateralis	M. ventrilateralis brevis internus	M. syringeus ventrilateralis internus (brevis)
M. sternotrachealis	M. sterno-trachealis	M. tracheo-clavicularis	not mentioned	M. sternotrachealis

4) M. bronchialis anticus occupies the ventral and ventrilateral regions of the syrinx, originating on the anterior edge of the ventral and ventrilateral surfaces of the drum, and sometimes on the elements anterior to the drum. More often than not the muscle has the following two well-differientiated fasciculi:

pars medialis. Most of this fasciculus originates ventrally on the medial side of M. bronchotrachealis anticus. The insertion is on the ventral end of A-2, sometimes also on A-3. The pars mediales of the two muscles may be in contact at the ventral midline or widely separated.

pars lateralis, This fasciculus originates lateral to the origin of the pars medialis, usually in continuity with the latter. It extends posteroventrad to insert near the ventral end of A-1 just dorsal to the insertion of M. bronchotrachealis anticus.

The fasciculi of M. bronchialis anticus may appear as two muscles with separate origins and insertions, as a single band with continuous origin and insertion, or as one of any number of intermediates.

THE OSCINE SYRINX, EXEMPLIFIED BY *CORVUS*.

Specimens Examined.

The genus *Corvus* is described as typical because it represents the syringeal structure of a large majority of oscines, because it is readily available to most anatomists, and because it has been the basis for most previous systems of nomenclature. I have examined the following 16 specimens of four species of *Corvus* and one species of *Pica:*

Corvus brachyrhynchos Brehm, 11 specimens
Corvus corone Linnaeus
Corvus macrorhynchos Wagler
Corvus ruficollis Lesson
Pica pica (Linnaeus), two specimens

I know of the following descriptions by previous authors:

Corvus brachyrhynchos Brehm — MacGillivray (1838)
Corvus brachyrhynchos Brehm — Maynard (1926)
Corvus brachyrhynchos Brehm — Miskimen (1951)
Corvus brachyrhynchos Brehm — Chamberlain et al. (1968)
Corvus corax Linnaeus — Yarrell (1833)
Corvus corax Linnaeus — Owen (1866)
Corvus corax Linnaeus — Fürbringer (1888)
Corvus corax Linnaeus — Haecker (1900)
Corvus corone Linnaeus — MacGillivray (1839)
Corvus corone Linnaeus — Gadow and Selenka (1893)
Corvus corone Linnaeus — Mayr (1931)
Pica pica (Linnaeus) — Wunderlich (1886)
Pica pica (Linnaeus) — Setterwall (1901)

Cartilaginous Elements.

The A-elements of *Corvus* (Pl. 21, figs. 3 and 4) consist of three divided elements (A-1 through A-3), a drum of four wholly fused complete elements (A-4 through A-7), and the remaining unmodified complete elements. A-1 is straight, except for the dorsal third, which is bent slightly posteriad. It is dorsoventrally oriented. A-2 is concave posteriorly, especially at the ventral end, and is round in cross section except at the ends, which are spatulate. A-3 is closely fitted to the posterior edge of A-4 for its full length.

A-4 through A-7 are complete elements wholly fused into a drum. In most individuals the outlines of the original elements are visible. The pessulus is fused to A-4 at both ends. It is triangular in cross section and bears a small anteriorly directed vane, the Membrana semilunaris.

All of the B-elements are divided and lie in planes perpendicular to the bronchial axes. Each has an ossified cap covering the center third of the element.

All of the previous descriptions of corvids agree with the above in the essential points, except those by MacGillivray (1838, 1839). He described only the last two "tracheal" elements as divided ("dimidiate") yet from his muscle descriptions the two divided elements are plainly A-1 and A-2. Apparently MacGillivray believed A-3 to be part of the drum, to which it is attached with dense fibrous connective tissue. Chamberlain et al. (1968) found that the drum in their specimens (55 in number) comprised five elements. The basis for this apparent variation needs further investigation.

Musculature.

The syringeal muscles of *Corvus* are, for the most part, distinct from one another at their edges.

M. tracheolateralis covers the dorsal two-thirds of the trachea, inserting on the syringeal aponeurosis and on elements A-10 laterally, A-9 dorsolaterally, and A-8 and A-7 dorsally.

M. sternotrachealis originates on the inner surface of the coracoid process of the sternum and inserts on the lateral surfaces of A-8 and A-9.

M. bronchotrachealis posticus originates on the posterior surface of the syringeal aponeurosis and on A-11 laterally, A-10 dorsolaterally and A-9 and A-8 dorsally. It extends posteriad, covering the dorsal surface of the trachea in a thin sheet and inserts on the dorsal ends of A-2 and A-3, and on the connective tissue between the two elements and between A-3 and A-4. The two Mm. bronchotracheales postici touch at the dorsal midline.

M. bronchotrachealis anticus originates on the posterior surface of the syringeal aponeurosis, ventrally adjacent to the origin of M. bronchotrachealis posticus, and on the ventrilateral surfaces of A-13 and A-12. It extends posteriad to insert on the ventral ends of A-1 and A-2.

M. bronchialis posticus originates on A-7 and A-8 laterally and on A-7 dorsolaterally. It extends posterodorsally to insert on the dorsal ends of A-2 and A-3 just ventral to the insertion of M. bronchotrachealis posticus.

M. bronchialis anticus has two well-differentiated fasciculi. They are in contact at their origins but separate at insertion. The pars medialis originates on the ventral surface of A-7 and on the ventrilateral surface of A-8. It extends posteriad on the medial side of M. bronchotrachealis anticus and beneath the latter muscle, to insert on the ventral end of A-2. The pars lateralis originates on the lateral surface of A-8 immediately posterior to the insertion of M. sternotrachealis. It extends posteriad, superior to the insertion of M. bronchialis posticus, and inserts on A-1 immediately dorsal to the insertion of M. bronchotrachealis anticus.

TABLE 5. Numbers of individuals, species, and genera of the suborder Passeres examined in this study.

	Out of a total of:		I have examined:		
Family	SPECIES	GENERA	SPECIMENS	SPECIES	GENERA
Alaudidae	76	15	15	9	6
Hirundinidae	78	19	21	16	11
Campephagidae	69	9	8	8	6
Dicruridae	20	2	6	4	2
Oriolidae	26	2	4	4	2
Corvidae	100	26	31	17	13
Cracticidae	10	2	2	2	2
Grallinidae	4	3	2	2	2
Ptilonorhynchidae	18	8	2	2	2
Paradiseidae	43	22	2	2	2
Paridae	65	9	5	5	4
Hyposittidae	1	1	1	1	1
Sittidae	17	3	13	10	3
Certhiidae	17	5	6	3	3
Chamaeidae	1	1	1	1	1
Timaliidae	251	64	32	31	21
Paradoxornithidae	12	2	3	3	2
Pycnonotidae	120	15	19	18	8
Chloropseidae	14	3	5	4	3
Cinclidae	4	1	2	2	1
Troglodytidae	59	14	13	9	7
Mimidae	27	13	9	9	8
Turdidae	307	48	67	59	26
Zeledoniidae	1	1	1	1	1
Sylviidae	398	85	51	50	32
Regulidae	5	1	4	2	1
Muscicapidae	328	56	45	45	27
Prunellidae	11	1	4	3	1
Motacillidae	48	5	5	4	2
Bombycillidae	4	2	5	2	1
Ptilogonatidae	4	3	3	3	3
Dulidae	1	1	4	1	1
Artamidae	10	1	3	3	1
Vangidae	12	8	8	8	6
Laniidae	65	10	10	10	7
Prionopidae	9	2	5	5	2
Cyclarhidae	2	2	1	1	1
Vireolaniidae	2	2	1	1	1
Callaeidae	3	3	none	—	—
Sturnidae	109	26	27	24	15
Meliphagidae	160	65	13	13	11
Nectariniidae	105	5	4	4	4
Dicaeidae	54	7	4	4	3
Zosteropidae	80	10	8	8	4
Vireonidae	37	4	5	5	3
Coerebidae	36	12	4	4	4
Drepanididae	22	9	7	7	5
Parulidae	119	18	21	20	14
Ploceidae	313	40	11	4	4
Icteridae	94	35	12	7	6
Tersinidae	1	1	1	1	1
Thraupidae	222	61	18	16	14
Catamblyrhynchidae	1	1	none	—	—
Fringillidae	412	120	61	55	48
TOTALS	4007	884	615	533	359

When allowance is made for differences in nomenclature, most of the previous descriptions agree with the above. An exception is the work of Gadow and Selenka (1893), but the disagreement stems from errors in the illustrations. Comparison of the three views of the oscine syrinx (figs. 62-64) with the text (p. 732) makes it evident that muscle numbers 2 and 3 are reversed in the ventral view; number 5 in the dorsal view should be number 3; number 6 in the dorsal view should be number 4; and muscle number 4 in the ventral view is apparently intended to represent number 6, but is misdrawn.

THE SYRINX IN OTHER OSCINE GROUPS.

Specimens Examined.

Of approximately 4000 species in about 884 genera contained in the 54 oscine families, I have examined 615 specimens in 533 species and 359 genera. Only two families, the Callaeidae and the Catamblyrhynchidae, are unrepresented in this assemblage. The relative coverage of the various families is shown in Table 5.

Cartilaginous Elements.

A detailed description of the cartilages in each of the oscine genera examined is beyond the scope of this study. With few exceptions, the pattern found in *Corvus* is nearly identical to that of all other genera. As noted by MacGillivray (1839) and by many subsequent authors, the pessulus is lacking in larks (Alaudidae). The only other major structural variant at the family level is the presence of some double B-elements in the swallows (Hirundinidae), except *Pseudochelidon* (Mayr and Amadon, 1951).

Musculature.

In all the oscines examined, the same two pairs of extrinsic and four pairs of intrinsic muscles are present, but there is much variability in the relative positions, size, and attachment of the muscles. Certain families show consistency in syringeal myology and these will be discussed in detail in later papers. I am unable to support the findings of Miskimen (1951) who reported M. bronchialis posticus absent in about 20 of the 29 oscines examined and M. tracheolateralis absent in 10 of the 29. No other author has reported either muscle to be lacking in any oscine. Comparison of my findings with those of Setterwall (1901) and Köditz (1925) leads to the conclusion that the oscine syringeal musculature is far more uniform than is suggested by many recent authors, who base their conclusions on the numbers of muscles described without evaluating the nomenclatorial principles behind the descriptions.

SYRINGEAL DEVELOPMENT

Although the embryology of the syrinx is well understood for some nonpasserine species, such as the domestic duck (*Anas*) and the chicken (*Gallus*), it is virtually unknown for passerines. Wunderlich (1886) provided a brief account of the embryology of the oscine syrinx in the House Sparrow (*Passer domesticus*), but he concerned himself only with the timing of various developmental stages.

The embryos and nestlings described below were dissected primarily to obtain data on posthatching changes in syringeal structure and secondarily to elucidate the developmental homology of syringeal muscles. In each specimen the syrinx was removed from the specimen and examined with a dissecting microscope. The syringes of eight Phoebes (*Sayornis*) and two Cowbirds (*Molothrus*) were sectioned and stained. Four separate staining methods were used (Gurr, 1955): Haematoxylin and Eosin; Foot's modification of the Masson Trichrome stain; Phosphotungstic Acid; and Von Kossa's stain for calcium.

SUBORDER TYRANNI.

SUPERFAMILY FURNARIOIDEA.

FAMILY FURNARIIDAE.

Specimens Examined.

The following three individuals were obtained from the New York Zoological Society. It is uncertain whether they are from the same or separate nests.

Synallaxis cinnamomea Lafresnaye	embryo; NYZS (no number); British Guiana; date unknown; Coll: C.W. Beebe; age (estimated): 1 day prehatching.
Synallaxis cinnamomea Lafresnaye	nestling; NYZS nestling "a"; British Guiana; date unknown; Coll: C.W. Beebe; age (estimated): 1 day posthatching.
Synallaxis cinnamomea Lafresnaye	nestling; NYZS nestling "b"; British Guiana; date unknown; Coll: C.W. Beebe; age (estimated): 2-3 days posthatching.

Cartilaginous Elements.

The three specimens are nearly identical in terms of the configuration of both A- and B-elements and are much like the adult of *Synallaxis cinerascens*. All of the elements are of soft cartilage and are strongly rounded like the B-elements of the adult. The membranes between them are extremely narrow; most of the consecutive elements are in contact. The Processi vocales are present, but the Membranae tracheales are not, all of the A-elements being of uniform width.

Musculature.

The muscles of the embryo and nestlings are exact miniatures of those of the adult *S. cinerascens*, originating and inserting on the same elements as in the latter.

SUPERFAMILY TYRANNOIDEA.

FAMILY COTINGIDAE.

Specimens Examined.

Only the following individual was obtained:

Platypsaris aglaiae (Lafresnaye)	nestling, YPM 1532; Mexico, Vera Cruz; 30 Jun 1961; Coll: R.W. Dickerman; age: 12-14 days posthatching.

Cartilaginous Elements.

The cartilaginous elements of the nestling differ from those of the adult only in being rounder in cross-section and proportionately closer together.

Musculature.

The musculature of the nestling is identical to that of the adult in shape and attachments.

FAMILY TYRANNIDAE.

Specimens Examined.

The specimens of *Sayornis* are not listed individually because they vary only in age.

Sayornis phoebe (Latham)	14 embryos, 3 nestlings; U.S.A., Conn.; May 1961; Coll: P. L. Ames; ages: 6 days prehatching to 8 days posthatching.
Fluvicola pica (Boddaert)	embryo; NYZS; no data; Coll: C. W. Beebe; age: 1-2 days prehatching.
Fluvicola pica (Boddaert)	nestling; NYZS; no data; Coll: C. W. Beebe; age: 1-3 days posthatching.
Fluvicola pica (Boddaert)	nestling; NYZS; no data; Coll: C. W. Beebe; age: 4-6 days posthatching.
Pitangus sulphuratus (Linnaeus)	nestling; NYZS; British Guiana; date unknown; Coll: C. W. Beebe; age: 8-10 days posthatching.

Cartilaginous Elements.

In *Sayornis* the cartilages begin to form as condensations of the mesenchyme of the respiratory tract late in the sixth or early in the seventh day of the fourteen-day incubation period. I could find no evidence that the formation of an element begins with one particular region or that a complete element is formed through the joining of halves of a divided one. By the eighth day all the cartilages are present, including the pessulus and the internal cartilages. The latter almost fill the medial surfaces of the short bronchi. At the end of the ninth or the beginning of the tenth day all the elements appear to have attained their ultimate configuration and further development is limited to changes in cross section and in consistency. The B-elements have attained their adult form by the hatching time but the A-elements are still soft and rounded. Staining shows no evidence of calcium deposition, even at two days posthatching. Calcium deposition in the adult syrinx is light and is limited to A-elements.

The specimens of *Fluvicola* and *Pitangus* show the same developmental pattern as comparable specimens of *Sayornis*. The two nestlings of *Fluvicola* are identical to each other, even in minute details. The embryo differs in the pattern of fusion and in lacking an extra component, A-3aR, possessed by the others.

Musculature.

In *Sayornis,* M. tracheolateralis and M. sternotrachealis appear about the beginning of the ninth day. In its earliest recognizable state M. sternotrachealis is attached directly to the trachea, not continuous with M. tracheolateralis as in *Gallus* and many other non-passerines. M. obliquus ventralis appears about a day after the other two muscles. Its fibers appear to develop in the mesenchyme of the ventral surface of the trachea. In 11-day embryos there are only transverse fibers, with no evidence of deep midventral attachment. At 12 or 13 days both of the adult muscle layers are present. At hatching the musculature is identical to that of the adult, but proportionately thinner.

The embryo and nestlings of *Fluvicola pica* are identical to the adult of *F. climazura* except that the muscles are proportionately thinner. The difference in muscle development is particularly evident in *Pitangus*, in which the flatness of the nestling M. obliquus ventralis contrasts with the prominent bulging of the adult muscle.

SUBORDER PASSERES.

Specimens Examined.

I have examined the following 16 embryos and 5 nestlings in 8 genera and 7 families. All of the specimens are in the YPM alcohol collection, but only the nestlings have catalogue numbers. Unless indicated as "measured," ages are estimated by comparison with embryos of known ages. Embryos whose ages are given as "measured" were obtained as freshly laid or slightly incubated eggs and were incubated in a forced-air incubator (37.5°C, 90 percent RH), giving an accuracy of approximately ± 12 hours to age determinations.

FAMILY CORVIDAE.

Corvus corone Linnaeus	nestling; YPM 4482; Aegean, Cyclades Is.; 6 Jun 1959; Coll: G. E. Watson; age: about 10 days posthatching.

FAMILY TROGLODYTIDAE.

Troglodytes troglodytes (Linnaeus)	nestling; YPM 4485; Canada, Quebec; 5 Aug 1949; Coll: S. C. Ball; age: about 10 days posthatching.

Thryothorus griseigularis	embryo; NYZS; British Guiana; 13 Oct 1920; Coll: C. W. Beebe; age: about 1 day prehatching.
FAMILY TURDIDAE.	
Turdus migratorius Linnaeus	2 embryos, 1 nestling; YPM; USA, Conn.; May, 1961; Coll: P.L. Ames; ages: 1 and 3 day prehatching and 2-3 days posthatching.
FAMILY NECTARINIIDAE.	
Cyanomitra dussumieri (Hartlaub)	embryo; YPM; Indian Ocean, Praslin Is.; 23 Jan 1958; Coll: W. D. Hartman; age: 3-4 days prehatching.
FAMILY PLOCEIDAE.	
Passer domesticus (Linnaeus)	3 embryos; YPM; USA, Conn. May, 1961; Coll: P. L. Ames; age: all 2-3 days prehatching, measured.
FAMILY ICTERIDAE.	
Quiscalus quiscala (Linnaeus)	embryo; YPM; USA, Conn.; 24 May 1961; Coll: P. L. Ames; age: about 1 day prehatching.
Molothrus ater (Boddaert)	7 embryos, 2 nestlings; YPM; USA, Conn.; May, 1962; Coll: P. L. Ames; ages: 5-6 days prehatching to 4 days posthatching, measured.
FAMILY FRINGILLIDAE.	
Ammospiza caudacuta (Gmelin)	embryo; YPM; USA, Conn.; 9 Jun 1961; Coll: P. L. Ames; age: 2-3 days prehatching.

Cartilaginous Elements.

The development of syringeal elements was studied most thoroughly in *Molothrus*. The cartilaginous elements are fully present in the youngest embryo, aged approximately eight days. The elements that form the drum are not yet fused. In the course of the next 36 hours elements A-4 through A-7 are fused into the drum, in which joints remain for at least a week after hatching.

All of the other specimens are like the comparable stages of *Molothrus*.

Musculature.

In the eight-day embryo of *Molothrus* I was unable to discern any muscles in the syringeal area. The formation of fibers is rapid; in the later part of the ninth day the syringeal region is surrounded by a nearly continuous sheet of muscle. The Mm.

sternotracheales are visible, but the short intrinsic muscles have not yet formed. By the following day the musculature closely approximates the adult condition, all muscles being clearly visible. By the time of hatching the muscles have the same proportions as in the adult.

In all of the other specimens the development of syringeal musculature closely parallels that of *Molothrus*.

SUMMARY

The timing of the onset of syringeal development in the furnariid *Synallaxis* cannot be determined from available material. At hatching the syrinx is similar to that of the adult but lacks the dorsal and ventral attenuation of elements associated with the Membranae tracheales.

In the Tyrannoidea, if *Sayornis* is typical, the development of syringeal cartilages begins slightly more than halfway through the incubation period. The muscles are first visible about a day later. At the time of hatching the syrinx is identical to that of the adult, except that the A-elements are softer and more rounded, the membranes between elements very narrow, and the muscles less strongly developed. The developmental pattern in *Fluvicola* and *Pitangus* and in the cotinga *Platypsaris* seems to be identical to that of *Sayornis*.

In all of the oscines examined the syringeal cartilages begin their development a little more than halfway through the incubation period; the muscles appear about a day later. At the time of hatching the syrinx is identical to that of the adult, except that the drum is incompletely fused.

MORPHOLOGICAL VARIATION

In order to evaluate a taxonomic character, one must examine the type and degree of variation found at each taxonomic level at which the character is to be applied. For a given taxonomic level, the most important variation is that found in the next lower level. Although the main purpose of this study is to establish relationships among genera and higher categories, an effort has also been made to evaluate intraspecific variation.

INTRASPECIFIC VARIATION.

Intraspecific variation may take the form of geographical, sexual, seasonal, age, or random individual variation. Proper evaluation of each of these requires the examination of series of individuals identical in all other respects, or the examination of a single large series of widely assorted individuals. Such series are not available in alcohol for any suboscine species, but in several species sufficient individuals were examined to allow estimates of the degree of uniformity present. Comparison of even as few as four or five individuals of a species gives an indication of the type and extent of variation present, to the extent that different ages, sexes and geographical regions are represented, although satistical reliability is not to be expected.

Intraspecific variation was studied to a limited degree in the antbird *Formicarius analis* (four specimens) and *Conopophaga lineata* (four specimens), the cotinga *Rhytipterna holerythra* (four specimens), and the tyrannids *Pyrocephalus rubinus* (five specimens) and *Tachuris rubrigastra* (four specimens). In 19 other species three individuals were examined and in 43 species two individuals. In most cases geographical and seasonal data are available, but age and sex are known for very few. Information about syringeal changes with increased age was obtained from the study of embryos and early nestlings. It was not possible to obtain age data on any fully grown specimens, for there is no reliable method of aging suboscines, comparable to the use of skull ossification in oscines.

INTRAGENERIC VARIATION.

Intrageneric variation is usually easier to evaluate than intraspecific, because it is often easy to acquire individuals of many species of some large genera. When single or few individuals of several species are studied, the term "intrageneric" remains more appropriate than "interspecific," for the observed variation represents a combination of intraspecific and interspecific differences.

Inasmuch as the genus is an artificial and highly subjective category, whether a particular type and degree of structural variation is inter- or intrageneric is ultimately of less importance than its relation to other taxonomic characters, both syringeal and non-syringeal. The differences between *Elaenia flavogaster* and *E. gaimardi* are treated here as intrageneric, following Hellmayr (1927), but they would be intergeneric if one were to separate *E. gaimardi* in the genus *Myiopagis* as is done by many authors. The tyrannid genera *Pipromorpha* and *Mionectes,* although maintained by Hellmayr, were felt by him to be "doubtfully separable," a view shared by Todd (1921). Future authors will probably view the slight differences in syringeal structure as intra- rather than intergeneric.

VARIATION IN CARTILAGINOUS ELEMENTS.

Fusion of A-elements.

The degree of totality of fusion and the precise regions of fusion are variable within rather narrow limits at the intraspecific level. Up to the age of about a year, and possibly more in some groups, the degree of fusion may be correlated with age. Little variation in fusion was found in oscines after the first few months of age. The slow development of the Membranae tracheales in the furnariid *Synallaxis* suggests that fusion is delayed in members of the Furnarioidea. In some species in the Tyrannidae (*Leptotriccus sylveolus, Myiozetetes similis, M. cayanensis* and *Tolmomyias sulphurescens,* for example) individuals differ in that elements wholly or partially fused in one may be devoid of fusion in another. In the large majority of species in which two or more specimens were examined the general pattern of fusion was the same for all individuals of the species, the variation being limited to the number of fused elements and the degree of totality. In suboscine species whose syringes have many fused elements (the woodcreeper *Glyphorhynchus spirurus*, the manakin *Chiroxiphia caudata*, and various species of the flycatcher genus *Elaenia*) considerable fusion is present in all individuals, but the exact number of elements involved is often variable. In one of my two specimens of *Glyphorhynchus spirurus* the drum is of seven elements; in the other it is of four elements. In *Elaenia chiriquensis* one of the three individuals examined has a drum of three elements; in the other two it is of four elements. In all three the fusion is complete and the pessulus is fused to the posterior element of the drum (A-3).

The degree of fusion of elements may vary less within some genera than within certain species of other genera. Among the suboscines examined only *Tyrannus, Myiarchus, Myiozetetes* and *Elaenia* were available in sufficient numbers to allow even tentative estimates of both intrageneric and intraspecific variation and only in the last two genera was there significant fusion. In both *Myiozetetes similis* and *M. cayanensis* intraspecific variation equaled that found in the genus; individuals with no fusion and those with three fused elements were found in each species.

In *Elaenia* the degree of variation in the genus exceeded the slight amount (one element among the three specimens of *E. chiriquensis*) found in either of the two species represented by multiple specimens. There was, however, less variation in the amount of fusion among the 12 specimens of nine species in *Elaenia* than between the two individuals of *Leptotriccus sylveolus* studied. Apparently the functional significance of fusion is different in the two genera.

There appears to be little or no intraspecific or intrageneric variation in fusion of B-elements. This type of fusion was found only in *Tyrannus* and a few similar genera and in *Tyranniscus chrysops.*

In the oscines, the only observed fusion was that of the lower A-elements that comprise the drum. The composition of the drum appears to be uniform at least up to the generic level. The configuration of the drum was noted in only a few of the many oscines studied, as it was desirable to retain the muscles for future study.

CONFIGURATION OF INDIVIDUAL ELEMENTS.

The number of divided, double or incomplete elements present is often subject to intraspecific variation. The type and extent of variation of a given element depends strongly on the configuration of adjacent elements. In the tyrannid *Colopteryx*, in which there is a long series of dorsally incomplete elements (A-5 through A-12 in my specimen), A-8 may be considered to be uniform. Since the length of the series of incomplete elements is variable—in Müller's specimen it extended through A-16—the configuration of A-13 or A-14 is undoubtedly variable. The variation present is really in the length of the dorsal "slot" complex, expressed in the configuration of the individual element. In *Empidonax minimus* A-5 is complete in two of the three specimens and incomplete dorsally in the third, A-4 being divided and A-6 complete in all three. Similar variation occurs in the Furnarioidea. As well as variation in the configuration of elements, there are differences in the degree of attenuation of elements at the anterior edges of the Membranae tracheales.

In short, the most variable region in the suboscines is the point of change from the divided A-elements at the posterior end of the syrinx (A-1 invariably being divided) to the complete anterior elements. An element is more likely to vary between divided and incomplete than between divided and complete and none was found to vary between dorsally and ventrally incomplete. There is a continuum from divided through incomplete to complete. The double condition may be considered to lie on the opposite side of divided from the "incompletes," there being no case of an element varying between double and incomplete. Double and divided configurations for the same element are found within a species (*Pyrocephalus rubinus*) or a genus (*Myiarchus*). In one specimen of *Pyrocephalus* A-4 is intermediate between divided and double, extending partway across the internal tympaniform membrane from the dorsal edge.

The configuration of cartilaginous elements in oscines appears to be uniform, even in small details, among individuals of a species and species of a genus. This is consistent with general homogeneity of the syrinx among the oscines.

SHAPE OF ELEMENTS.

In general the proportions and contours of a given element are variable in suboscines, even at the intraspecific level. Variation is not extreme, however, being limited to the degree of spatulation, of rounding, or of other modifications. The contours of a given element appear to be influenced by the shapes and, particularly, the positions of adjacent elements. If the ends of an incomplete element meet in line with each other, they are likely to be squared off (e.g. *Tyrannnus,* Pl. 10) ; if they are not aligned, but each end lies opposite a space, they are more apt to be pointed (see *Legatus,* Pl. 7). The latter case is of common occurrence when strong asymmetry is present.

There is little variation in the shapes of elements that bear muscle insertions. A-1 and B-1 are relatively uniform up to the generic level. Other elements may also exhibit great uniformity. In the large cotinga, *Pyroderus,* the sculptured edges of the lower A-elements are virtually identical in my two specimens and that examined by Garrod (1878).

In the pittas and some broadbills, the lower A-elements have irregular edges and frequent holes (membranous, of course). I have not examined more than one specimen in any species of the genus *Pitta,* but at the intrageneric level these irregularities appear to be randomly distributed.

ASYMMETRY.

Various degrees of bilateral asymmetry are found in many suboscine syringes. The most common and most variable type of asymmetry involves the width or shape of an element. The opening of a divided or dorsally incomplete element is frequently displaced from the midline, usually to the left. Displacement at the ventral midline is rare.

Asymmetrical fusion is of frequent occurrence in the superfamily Tyrannoidea, but appears to be individually variable. Twenty-one individuals of 20 genera were found to possess unequal fusion. In most cases the fusion is partial, often involving only the ends of two elements. Often the pessulus is involved. In the flycatcher *Myiophobus*, (Pl. 20) the pessulus in the only specimen examined is fused dorsally to A-4 on the right and to A-5 on the left. In many other examples the pessulus is fused only to one side of one element. Of the 20 genera in which unequal fusion was found, two or more specimens were examined in 13. Two of seven individuals of *Myiozetetes* were asymmetrical in this respect, but in several other tyrannid genera of which seven or more specimens were examined (*Tyrannus, Myiarchus, Elaenia*) no asymmetry was found. In other respects the cartilaginous structure of *Myiozetetes* shows much more variation than the other genera. It thus appears that the tendency toward asymmetry, as well as other types of variation, is greater in some genera than in others.

Less asymmetrical fusion was found in the superfamily Furnarioidea than in the Tyrannoidea. What asymmetry there is appears limited to the elements posterior to the Membranae tracheales (e.g. *Taraba,* Pl. 3).

The most extreme form of asymmetry found in the suboscine syrinx is the presence of an "extra" component on one side. Extra components were found in 17 individuals of 11 genera in the Tyrannoidea. None were found in any genus of the Furnarioidea or of the suborders Eurylaimi, Menurae, or Passeres. It is noteworthy that in every case the extra component is on the right side. This uniformity suggests a functional significance of the extra element, perhaps correlated with the slight but regular bend of the trachea to the left in the region of the syrinx. The distribution of extra components appears to be less individually variable than other forms of asymmetry. Both specimens of *Onychorhynchus* and of *Habrura,* all three specimens of *Microtriccus,* and three out of four specimens of *Pitta* have extra components. Long series of several of these genera should be examined to evaluate fully the degree of variation in this form of asymmetry.

PESSULUS.

The degree of variation in the pessulus is itself highly variable, correlated with the overall variation in the structure of the syrinx. All members of the suboscine superfamily Furnarioidea and all of the oscine family Alaudidae (larks) lack the pessulus entirely. In the superfamily Tyrannoidea specimens of 24 genera in four families were found lacking the pessulus. In most of the tyrannoid cases the anterior ends of the internal tympaniform membranes, which are usually attached to the pessulus, are attached to some other form of cartilage, the shape of which varies greatly. Such cartilages are also found in many syringes possessing pessuli.

In 21 genera of the Tyrannidae specimens were found lacking the pessulus. In three of these genera (*Tyrannus*, *Myiobius* and *Empidonax*) individuals both with and without pessuli were found, and the number of such genera might well be higher if large series of some other genera were examined. Of three specimens of *Tyrannus tyrannus* from the same locality in Connecticut, two have the pessulus, one does not.

Despite the variability of the pessulus down to the level of populations, the range of variation within a species or a genus is limited. When the pessulus is entirely lacking in some individuals (or species), it is present only in form of a short bar or one incompletely fused in the remainder of the species (or genus). In no genus were individuals without pessuli and those with completely fused pessuli found.

CARTILAGINOUS PLUG OR SHEET.

There is little intraspecific or intrageneric variation in the presence or absence of a dorsomedial plug or sheet. The contours of this cartilage seldom show differences among members of a well-defined genus.

Other areas of soft cartilage joining A-elements, such as are present in the tyrannid *Tachuris* and the antbird *Formicarius*, were found to be highly uniform within the small series of specimens examined.

INTERNAL CARTILAGES.

Found only in tyrant flycatchers, some cotingas, the sharpbill (*Oxyruncus*), and one genus each of manakin (*Schiffornis*), asity (*Neodrepanis*), and New Zealand wren (*Acanthisitta*), internal cartilages are among the most uniform of cartilaginous components at the intrageneric level. Members of a species have similar but not always identical internal cartilages. Both J- and ⅃-shaped cartilages are found in the same species and the proportions of bars and triangles vary intraspecifically, but rounded triangles were not found in the same species or even in the same genus as J-shaped cartilages. The more intricate shapes, such as those in *Corythopis*, *Leptopogon*, *Platyrinchus*, and *Pipromorpha,* are subject to even less variation than the simpler ones.

The number of pairs of internal cartilages was also uniform, being one in most genera. Of the genera possessing two pairs, only *Myiarchus* was studied in sufficient depth to allow an estimate of the degree of variation to be expected. In all seven individuals of five species there were two pairs of internal cartilages present and these were uniform in shape and position.

The only genus examined with variation in the number of internal cartilages is *Tolmomyias*. The two species examined differ so much that only the study of a larger series of specimens will permit evaluation of the variation present.

MUSCULATURE.

M. TRACHEOLATERALIS.

In this study I have concerned myself only with the position, width and insertion of this muscle. The position and width are extremely uniform up to the generic level, the only exception being the tyrannid genus *Tolmomyias*, which is also variable in other aspects of the syrinx. In suboscines the degree of variation of the insertion of M. tracheolateralis is correlated with the presence of intrinsic muscles. When none are present, as in the Eurylaimidae, some of the Furnarioidea, and many of the Tyrannoidea, it inserts near the A-B junction, the mode and place of insertion being intragenerically uniform. An exception is the broadbill genus *Smithornis*, in which the insertion is higher on the trachea and the precise element of insertion apparently variable.

In the presence of intrinsic musculature the exact region of insertion of M. tracheolateralis is more variable than when no intrinsic muscles are present, but the variation is not extreme. When the insertion is immediately anterior to the origin of the intrinsic muscles, as in many tyrannid flycatchers, there is seldom more than one or two elements' variation in its position.

The degree of variation is related to other features of the syrinx. When a well-developed drum is present, M. tracheolateralis usually inserts on its anterior edge, but the number of elements comprising the drum may be variable (see above). Where it interacts with the intrinsic muscles, M. tracheolateralis shows considerable uniformity. It was found to be constant in several species of *Empidonax* and *Myiochanes*, in which it extends beneath the intrinsic muscle to insert on A-2, and in *Leptopogon* and *Pyrocephalus*, in which it extends posteriad between the ventral intrinsic muscles.

M. STERNOTRACHEALIS.

The mode of insertion of this muscle appears to be uniform well above the generic level in the superfamily Furnarioidea and the suborder Passeres. Considerably more variation is found in the Tyrannoidea.

In most genera of the Tyrannidae the type of insertion of M. sternotrachealis is related to the relative cross-sectional area of the muscle, which is approximately uniform within most of the genera studied. A thick muscle usually inserts by two or three fasciculi, each with a different type of insertion. In some individuals of a genus (or on one side of an individual only) a fasciculus may be entirely missing. The proportions of the various fasciculi may vary greatly within a species, as may the anteroposterior position of the insertion. The most variable form of insertion, in terms of presence or absence, is that of continuity with M. tracheolateralis, but when only this form of insertion is present it is more uniform.

The anteroposterior position and the area covered by the insertion appear to vary most when all or nearly all of the muscle inserts directly. In *Myiarchus,* for example, the most posterior element of insertion varies from A-11 to A-15. In this case the variation appears to be interspecific, but similar variation in *Myiozetetes* seems to be intraspecific. The samples on hand are too small for positive determination of the basis of variation.

In summary, M. sternotrachealis displays a rather uniform appearance within a genus of tyrant flycatchers. This uniformity is reflected in the general proportions of the muscle and in the type of insertion. In the anteroposterior position of its insertion the muscle is quite variable.

In other families of the Tyrannoidea few individuals of most genera were examined. In the becards of the genus *Pachyramphus* the situation is like that of the Tyrannidae. In the Furnarioidea there is less variation at the intrageneric level, but the exact position of the insertion is often variable. In *Conopophaga* whether the muscle inserts partly on the Processus vocalis or wholly on the trachea is intraspecifically variable. The position of the insertion of M. sternotrachealis is much more uniform in the oscines, up to the family level.

Intrinsic Muscles.

There are several sources of potential variation in the intrinsic musculature, principally the mode and position of the origin and insertion and the general shape of the muscle.

In the superfamily Tyrannoidea intrinsic muscles are found only in a few cotingas and manakins, the sharpbill, and most of the tyrant flycatchers. In all cases in which more than one member of a species was examined the mode and position of origin was found to be intraspecifically uniform. With very few exceptions, the uniformity extends to the generic level. In some of the exceptions (*Pitangus, Tolmomyias, Tyranniscus*) the variation in intrinsic muscles was accompanied by interspecific differences in other features of the syrinx. In other genera the variation, although clearly visible, was restricted to a particular aspect of the musculature. In *Pyrocephalus rubinus* there is an unusually large amount of individual variation in the width of the intrinsic muscle, M. obliquus ventralis. In *Sayornis* there is intrageneric variation in the presence of transverse continuity of the superficial muscle layer. In *Elaenia* there is variation, apparently interspecific, in the mode of origin of M. obliquus ventralis. In the last genus there is some intrageneric variation in the degree of separation of the lateral muscle from the ventral one.

The mode of insertion of an intrinsic muscle is more subject to intrageneric variation than the mode of origin, but most of the differences are quantitative. In *Suiriri* and *Phaeomyias* the width of the tendon of M. obliquus ventralis is variable, while in *Elaenia* the mode of insertion, tendinous or direct, and the element of insertion are variable. In most of the genera of tyrant flycatchers in which individuals of several species were examined (*Xolmis, Tyrannus, Myiarchus, Empidonax*) the shape and attachment of the intrinsic muscles were found to be highly uniform at the generic level.

In the Furnarioidea and the Passeres the intrinsic muscles are more uniform than in the Tyrannoidea. In the Formicariidae and Furnariidae there is intrageneric variation in muscle origins, comparable to that found in the Tyrannidae, i.e. positional differences of one or two elements, without differences in the interrelationships of the various muscles. Not even this much variation has been found in any genus of the suborder Passeres.

MORPHOLOGICAL SUMMARY

The major structural features of the syringes examined in this study are summarized in the following compilations. The first outline summarizes the distribution of individual syringeal features. Because of fundamental and consistent differences between the "tracheophone" type of syrinx, with Membranae tracheales and associated structures, and the type found in the rest of the passerines, I have divided the detailed compilation into two categories, those with and those without Membranae tracheales. Within each category the structural variations are differentiated in as much detail as is feasible. In some features of the syrinx, such as the degree of fusion of elements or the positions of muscle origins, the number of variations is so great and the differences between adjacent members of the morphological series so slight that grouping into many small categories would create an artificial and unreal order. To minimize this artificiality, I have avoided a detailed summary of features with many subtle variations and have established instead broad categories which indicate the relative degrees to which a feature is present. The positions of muscles relative to the planes of symmetry of the syrinx are more uniform and the morphological variations more easily classified. Within each morphological division, taxonomic groups are listed in the conventional order, as in earlier sections.

When specimens of a taxonomic group fall into more than one division of a structural feature the taxonomic name is followed by "(part)" and placed in each appropriate section. Inasmuch as most genera are represented in this study by only single specimens, predictably few are listed under more than one heading. The variation found in a given structural feature is best understood by observing the distribution of genera, such as *Tyrannus, Myiarchus* and *Elaenia,* in which several individuals and species were examined.

DETAILED SUMMARY OF MORPHOLOGY.

Category I. Lower trachea dorsoventrally compressed; elements in compressed region attenuated and sometimes absent, forming dorsal and ventral "windows" or Membranae tracheales; lateral cartilaginous or bony rods or plates (Processi vocales) present; pessulus absent.

Suborder Tyranni (part) : Superfamily Furnarioidea

A. Cartilaginous elements.

1. Fusion of elements.
   a. No fusion.
      Furnariidae (part) : *Asthenes, Automolus, Geositta, Sclerurus.*

Rhinocryptidae (part) : all except *Melanopareia.*
Formicariidae.

b. Two or more elements fused, forming a "drum".
Dendrocolaptidae.
Furnariidae (part) : all except those in (a), above.
Rhinocryptidae (part) : *Melanopareia.*

2. Processi vocales.

a. Very small; attached to surrounding elements by fibrous connective tissue.
Formicariidae (part): all except *Formicarius, Chamaeza, Grallaria,* and *Conopophaga.*

b. Prominent straight bars, thicker than those in (a), rather uniform in width.
Formicariidae (part) : *Formicarius, Chamaeza, Grallaria, Conopophaga.*
Rhinocryptidae (part) : *Teledromas.*

c. Wide base; narrow "stalk"; flat, flared anterior end.
Furnariidae (part) : all except *Geositta.*
Rhinocryptidae (part) : all except *Teledromas.*

d. Wide base; broad central part; prominent dorsal and ventral horns.
Dendrocolaptidae.
Furnariidae (part) : *Geositta.*

B. Musculature.

1. Extrinsic muscles (two pairs present in all passerines).

a. M. tracheolateralis.

i. Width (approximate average along the 12 elements immediately anterior to the Membranae tracheales).

a) Narrow (each of the pair less than 30° of tracheal circumference in width).
Formicariidae (part) : *Formicarius, Grallaria, Conopophaga.*
Rhinocryptidae (part) : *Teledromas.*

b) Medium (30-60° of tracheal circumference).
Dendrocolaptidae.
Rhinocryptidae (part) : all except *Teledromas.*

c) Broad (more than 60° of tracheal circumference).
Furnariidae.
Formicariidae (part): all except *Formicarius, Grallaria* and *Conopophaga.*

ii. Insertion.

a) On the drum and/or other elements immediately anterior to the Membranae tracheales.
Dendrocolaptidae.
Furnariidae.
Formicariidae (part): *Cymbilaemus, Sakesphorus, Thamnophilus, Dysithamnus, Thamnomanes, Herpsilochmas, Neorhopias, Cercomacra, Pyriglena, Myrmoborus, Hypocnemis, Myrmeciza, Gymnopithys, Hylophylax.*
Rhinocryptidae (part) : *Pteroptochos, Rhinocrypta, Triptorhinus.*

b) On the anterior end of the Processus vocalis.
Formicariidae (part): *Formicarius, Grallaria, Conopophaga* (part).
Rhinocryptidae (part): *Scelorchilus, Teledromas, Melanopareia.*

c) On the drum and/or elements anterior to the Membranae tracheales *and* on the anterior end of the Processus vocalis.
Formicariidae (part): *Taraba, Pygiptila, Chamaeza, Conopophaga* (part).
Rhinocryptidae (part): *Scytalopus.*

d) On elements anterior to the Membranae tracheales and (superficial fibers) in continuity with M. sternotrachealis.
Formicariidae (part): *Myrmotherula, Myrmorchilus.*

b. M. sternotrachealis.

i. Type and region of insertion.

a) Directly on the anterior end of the Processus vocalis.
Dendrocolaptidae.
Furnariidae.
Formicariidae (part): *Formicarius, Chamaeza, Grallaria.*
Rhinocryptidae.

b) In part on the anterior end of the Processus and in part on the lateral surface of elements immediately anterior to the Membranae.
Formicariidae (part): *Conopophaga* (part).

c) On the lateral surfaces of several elements immediately anterior to the Membranae.
Formicariidae (part): *Conopophaga* (part).

d) By two fasciculi; one to the anterior end of the Processus; the other to the dorsolateral surfaces of the elements immediately anterior to the Membranae, inserting adjacent to the dorsal edge of M. tracheolateralis, or partially in continuity with that muscle.
Formicariidae (part): all except *Formicarius, Chamaeza, Grallaria* and *Conopophaga.* (Fiber continuity only in *Myrmotherula* and *Myrmeciza.*)

2. Intrinsic muscles.

a. Number present.

i. None.
Formicariidae (part): *Formicarius, Chamaeza, Grallaria, Conopophaga.*
Rhinocryptidae (part): *Teledromas.*

ii. One pair.
Formicariidae (part): all except *Formicarius, Chamaeza, Grallaria* and *Conopophaga.*
Rhinocryptidae (part): all except *Teledromas.*

iii. Two pairs.
Dendrocolaptidae.
Furnariidae.

b. Position of muscle origin.

i. When one pair present.

a) On the ventral and ventrilateral surfaces of several elements immediately anterior to the Membranae tracheales.
Formicariidae (part): all possessing intrinsic muscles.

b) On the lateral and/or dorsolateral surfaces of several elements immediately anterior to the Membranae tracheales.
Rhinocryptidae (part) : all possessing intrinsic muscles.

ii. When two pairs present.

a) Dorsal pair originates on the lateral and dorsolateral surfaces of the several elements anterior to the Membranae tracheales (on the anterior edge of the drum, when one is present) ; ventral pair originates on the lateral and ventrilateral surfaces of the same elements.
Dendrocolaptidae.
Furnariidae.

c. Position of muscle insertion.

i. When one pair present.

a) On the anterior end of the Processus, dorsally and anteriorly adjacent to the insertion of M. sternotrachealis.
Formicariidae (part) : all possessing intrinsic muscles.

b) On the anterior end of the Processus, ventrally adjacent to the insertion of M. sternotrachealis.
Rhinocryptidae (part) : all except *Teledromas* and *Melanopareia.*

c) Along nearly the entire length of the Processus.
Rhinocryptidae (part) : *Melanopareia.*

ii. When two pairs present.

a) Dorsal pair inserts on the anterior end of the Processus, posterodorsal to the insertion of M. sternotrachealis; ventral pair inserts on the anterior end of the Processus, posteroventral to the insertion of M. sternotrachealis.
Furnariidae (part) : all except *Geositta.*

b) On the dorsal and ventral horns, respectively, of the Processus.
Dendrocolaptidae.
Furnariidae (part) : *Geositta.*

CATEGORY II. Lower trachea cylindrical or nearly so. Membranae tracheales and Processi vocales absent.

Suborder Eurylaimi
Suborder Tyranni (part) : Superfamily Tyrannoidea
Suborder Menurae
Suborder Passeres

A. Cartilaginous elements.

1. Fusion of A-elements.

a. No fusion.

i. Membranous areas between elements.
Eurylaimidae (part) : *Smithornis, Cymbirhynchus, Eurylaimus.*
Cotingidae (part) : *Heliochera, Casiornis, Pheonicircus, Attila, Rhytipterna, Platypsaris, Pachyramphus, Iodopleura, Conioptilon.*
Pipridae (part) : *Piprites, Corapipo, Schiffornis, Ilicura.*

Tyrannidae (part): *Xolmis, Phaeotriccus, Knipolegus, Neoxolmis, Ochthoeca, Sayornis, Colonia, Gubernetes, Yetapa, Agriornis, Muscisaxicola, Lessonia, Entotriccus, Lichenops, Muscipipra, Fluvicola, Arundinicola, Pyrocephalus, Muscigralla, Satrapa, Machetornis, Myiozetetes* (part), *Mitrephanes, Myiophobus, Terenotriccus, Onychorhynchus, Aphanotriccus, Platyrinchus, Myiornis, Lophotriccus, Euscarthmornis, Colopteryx, Hemitriccus, Oncostoma, Leptotriccus* (part), *Todirostrum* (part), *Tachuris, Phyllomyias, Leptopogon.*
Oxyruncidae.
Phytotomidae.
Pittidae.
Philepittidae.

ii. Closely fitted or overlapping elements.
Eurylaimidae (part): *Psarisomus, Serilophus, Calyptomena.*
Cotingidae (part): *Cotinga, Xipholena, Euchlornis, Carpodectes, Tityra* (part), *Querula, Cephalopterus, Perissocephalus, Gymnoderus.*
Tyrannidae (part): *Pitangus, Empidonax, Blacicus.*

b. Partial fusion (less than the full length of any element).

i. Ventral and/or dorsal midline only.
Cotingidae (part): *Pyroderus, Laniocera.*
Tyrannidae (part): *Capsiempis, Colorhamphus.*

ii. More than midline, but not complete fusion.
Cotingidae (part): *Tityra* (part).
Tyrannidae (part): *Tyrannus, Muscivora, Myiodynastes, Tolmarchus, Megarhynchus, Conopias, Tyrannopsis, Legatus, Myiarchus, Eribates, Nesotriccus, Pyrrhomyias, Myiobius, Nuttallornis, Tolmomyias, Habrura, Phylloscartes, Leptotriccus* (part), *Todirostrum* (part), *Serpophaga, Corythopis, Spizitornis, Mecocerculus, Inezia, Stigmatura, Tyrannulus, Tyranniscus.*

c. Complete (full length) fusion of two or more elements.

i. Involving divided or double elements only.
Cotingidae (part): *Procnias.*
Pipridae (part): *Manacus.*
Tyrannidae (part): *Phaeomyias* (part).

ii. Involving complete elements, with or without other types of elements.
Cotingidae (part): *Rupicola.*
Pipridae (part): *Pipra, Chiroxiphia.*
Tyrannidae (part): *Empidonomus, Sirystes, Myiozetetes* (part), *Myiarchus* (part), *Cnemotriccus, Pseudocolopteryx, Euscarthmus, Elaenia, Suiriri, Phaeomyias* (part), *Microtriccus, Leptopogon, Pipromorpha, Mionectes.*

2. Fusion of B-elements.

a. B-1 and B-2 joined by a short bridge.
Tyrannidae (part): *Tyrannus, Muscivora, Empidonomus, Myiodynastes, Megarhynchus, Conopias, Tyrannopsis, Tolmarchus, Tyranniscus.*

b. B-3 and B-4 joined by a short bridge.
Tyrannidae (part): *Pitangus* (part).

3. Pessulus.
   a. Absent.
      Cotingidae (part) : *Tityra* (part).
      Pipridae (part) : *Chiroxiphia.*
      Tyrannidae (part) : *Xolmis, Knipolegus, Neoxolmis, Satrapa, Entotriccus, Lessonia, Tyrannus* (part), *Megarhynchus, Pitangus, Sirystes, Myiarchus, Myiobius* (part), *Nuttallornis, Empidonax* (part), *Aechmolophus, Platyrinchus, Phylloscartes, Serpophaga, Spizitornis, Mecocerculus, Inezia, Tachuris.*
      Pittidae (part).
      Suborder Passeres (part) : Alaudidae.
   b. Partial pessulus.
      Tyrannidae (part) : *Tyrannus* (part), *Legatus, Myiodynastes, Myiozetetes* (part), *Tolmarchus, Blacicus, Phyllomyias, Pittidae* (part).
   c. Full pessulus, but not wholly fused to other components.
      Cotingidae (part) : *Cotinga, Pyroderus, Procnias, Attila, Phoenicircus, Casiornis, Rhytipterna, Iodopleura, Laniocera, Pachyramphus* (part).
      Pipridae (part) : *Pipra, Manacus, Ilicura.*
      Tyrannidae (part) : *Arundinicola, Sayornis, Machetornis, Myiozetetes* (part), *Myiophobus, Terenotriccus, Onychorhynchus, Myiobius* (part), *Empidonax* (part), *Myiochanes, Tolmomyias, Rhynchocyclus, Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Habrura, Capsiempis, Pseudocolopteryx, Todirostrum* (part), *Stigmatura, Microtriccus, Leptopogon.*
      Oxyruncidae.
      Acanthisittidae.
   d. Full pessulus, fused to other components at both ends.
      Eurylaimidae.
      Cotingidae (part) : *Xipholena, Euchlornis, Lipaugus, Heliochera, Pachyramphus* (part), *Platypsaris, Tityra* (part), *Querula, Carpodectes, Cephalopterus, Perissocephalus, Gymnoderus, Conioptilon, Rupicola.*
      Pipridae (part) : *Piprites, Corapipo, Schiffornis.*
      Tyrannidae (part) : *Phaeotriccus, Pyrocephalus, Conopias, Mitrephanes, Pyrrhomyias, Cnemotriccus, Pogonotriccus, Todirostrum* (part), *Nesotriccus, Euscarthmus, Corythopis, Colorhamphus, Suiriri, Elaenia, Phaeomyias, Tyranniscus, Pipromorpha, Mionectes.*
      Phytotomidae.
      Philepittidae.
      Suborder Menurae.
      Suborder Passeres (part) : all except Alaudidae.

4. Cartilaginous plug or sheet, present only in the following:
   Cotingidae (part) : *Tityra.*
   Pipridae (part) : *Piprites.*
   Tyrannidae (part) : *Xolmis, Phaeotriccus, Pyrocephalus, Knipolegus, Neoxolmis, Gubernetes, Agriornis, Muscisaxicola, Satrapa, Entotriccus, Muscipipra, Yetapa, Colonia, Ochthoeca, Sayornis, Lichenops, Muscigralla, Megarhynchus, Legatus, Sirystes, Myiarchus, Eribates, Nuttallornis, Aphanotriccus, Empidonax, Blacicus, Mitrephanes, Stigmatura.*

5. Internal cartilages.
   - a. Absent.
     - Cotingidae (part): all except *Attila, Casiornis, Rhytipterna, Laniocera, Pachyramphus, Platypsaris* and *Iodopleura.*
     - Pipridae (part): all except *Schiffornis.*
     - Tyrannidae (part): *Colopteryx, Euscarthmornis, Hemitriccus, Oncostoma.*
     - Phytotomidae.
     - Pittidae.
     - Philepittidae (part): *Philepitta.*
     - Acanthisittidae (part): *Xenicus.*
     - Suborder Menurae.
     - Suborder Passeres.
   - b. Present.
     - i. Triangular.
       - Cotingidae (part): *Iodopleura.*
       - Tyrannidae (part): *Xolmis, Phaeotriccus, Knipolegus, Lichenops, Colonia, Sayornis* (part), *Nuttallornis, Aphanotriccus, Blacicus, Mitrephanes, Cnemotriccus, Tolmomyias* (part), *Colorhamphus.*
       - Philepittidae (part): *Neodrepanis.*
     - ii. Straight bars.
       - Cotingidae (part): *Pachyramphus, Platypsaris.*
       - Tyrannidae (Part): *Agriornis, Sayornis* (part), *Muscigralla, Arundinicola, Tyrannus, Myiodynastes, Pitangus* (part), *Myiozetetes, Nesotriccus, Myiochanes, Aechmolophus, Myiobius, Pyrrhomyias, Myiophobus, Tolmomyias* (part), *Myiornis, Habrura, Capsiempis, Pseudocolopteryx, Pogonotriccus, Phylloscartes, Euscarthmus, Serpophaga, Spizitornis, Mecocerculus, Inezia, Stigmatura, Phaeomyias, Tyrannulus, Phyllomyias, Tyranniscus, Leptopogon.*
       - Acanthisittidae (part): *Acanthisitta.*
     - iii. J- or ⅃-shaped.
       - Cotingidae (part): *Attila, Casiornis, Rhytipterna.*
       - Pipridae (part): *Schiffornis.*
       - Tyrannidae (part): *Pyrocephalus, Gubernetes, Satrapa, Entotriccus, Muscivora, Megarhynchus, Conopias, Pitangus* (part), *Legatus, Sirystes, Empidonax, Myiarchus, Eribates, Terenotriccus.*
     - iv. Other shapes.
       - Tyrannidae (part):
         - *Lessonia,* shield-shaped.
         - *Machetornis,* elliptical.
         - *Onychorhynchus,* peanut-shaped, with fat capsules.
         - *Platyrinchus,* straight bars with ⅃-shaped extensions.
         - *Rhynchocyclus,* S-shaped.
         - *Leptotriccus,* flattened spheres, each with one long stem.
         - *Corythopis,* flattened spheres, each with two long stems.
         - *Todirostrum,* straight sheets, fused to A-1 through A-5.
         - *Tachuris,* circular plates, with fat capsules.
         - *Elaenia, Microtriccus, Camptostoma,* straight or slightly curved bars, with semicircular ventrad extensions.

Pipromorpha, Mionectes, long, slightly curved blades, extending posteriad from flattened hemispheres, the whole connected to an A-element by a short stem.

Oxyruncidae: Long narrow, slightly curved bars.

v. Second (ventral) pair present.
Cotingidae (part): *Attila, Casiornis, Rhytipterna, Laniocera.*
Tyrannidae (part): *Agriornis, Arundinicola, Myiarchus, Tolmomyias* (part), *Rhynchocyclus, Todirostrum, Inezia, Tyrannulus.*

B. Musculature.

1. Extrinsic muscles: two pairs present in all passerines.

a. M. tracheolateralis.

i. Width (approximate average width along the 12 elements immediately anterior to insertion).

a) Narrow (each muscle less than 30° of tracheal circumference).
Eurylaimidae.
Cotingidae (part): *Phoenicircus, Heliochera, Cotinga, Xipholena, Tityra, Querula, Pyroderus, Cephalopterus, Perissocephalus, Conioptilon, Rupicola.*
Pipridae (part): *Piprites.*
Tyrannidae (part): *Ochthoeca, Myiodynastes, Pitangus, Legatus, Sirystes, Nesotriccus, Terenotriccus, Myiobius, Onychorhynchus, Rhynchocyclus, Tolmomyias, Todirostrum.*
Phytotomidae.
Pittidae.
Acanthisittidae.

b) Medium (30-60° of tracheal circumference).
Cotingidae (part): *Euchlornis, Lipaugus, Pachyramphus, Platypsaris.*
Pipridae (part): *Schiffornis.*
Tyrannidae (part): *Conopias, Myiozetetes, Pyrrhomyias, Oncostoma, Lophotriccus, Euscarthmornis, Colopteryx, Myiornis, Hemitriccus, Pogonotriccus, Stigmatura, Corythopis, Inezia, Colorhamphus, Leptopogon, Pipromorpha, Mionectes.*
Oxyruncidae.

c) Broad (more than 60° of tracheal circumference).
Cotingidae (part): *Attila, Laniocera, Rhytipterna, Gymnoderus, Casiornis, Iodopleura.*
Pipridae (part): *Pipra, Chiroxiphia, Corapipo, Manacus, Ilicura.*
Tyrannidae (part): *Agriornis, Xolmis, Muscisaxicola, Lessonia, Neoxolmis, Sayornis, Colonia, Gubernetes, Yetapa, Knipolegus, Phaeotriccus, Entotriccus, Lichenops, Muscipipra, Fluvicola, Arundinicola, Pyrocephalus, Muscigralla, Machetornis, Muscivora, Tyrannus, Empidonomus, Megarhynchus, Tyrannopsis, Tolmarchus, Myiarchus, Eribates, Nuttallornis, Myiochanes, Blacicus, Empidonax, Aechmolophus, Cnemotriccus, Mitrephanes, Aphanotriccus, Myiophobus, Platyrinchus, Tolmomyias* (part), *Leptotriccus, Phylloscartes, Capsiempis, Euscarthmus,*

Pseudocolopteryx, Habrura, Tachuris, Spizitornis, Serpophaga, Mecocerculus, Elaenia, Suiriri, Phaeomyias, Camptostoma, Phyllomyias, Tyranniscus, Tyrannulus, Microtriccus, Sublegatus.

Philepittidae.

Suborder Menurae.

Suborder Passeres.

ii. Position.

a) Members of the pair do not touch at the ventral midline.

Eurylaimidae.

Cotingidae (part): *Phoenicircus, Heliochera, Cotinga, Xipholena, Carpodectes, Euchlornis, Lipaugus, Tityra, Querula, Pyroderus, Cephalopterus, Perissocephalus, Gymnoderus, Conioptilon, Procnias, Rupicola.*

Pipridae (part): *Piprites, Schiffornis.*

Tyrannidae (part): *Legatus, Sirystes, Myiodynastes, Conopias, Myiozetetes, Pitangus, Myiarchus, Eribates, Nesotriccus, Terenotriccus, Aphanotriccus, Myiobius, Onychorhynchus, Tolmomyias* (part), *Rhynchocyclus, Todirostrum, Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Spizitornis, Elaenia* (part), *Suiriri, Sublegatus, Phaeomyias, Tyrannulus.*

Phytotomidae.

Pittidae.

Philepittidae.

Acanthisittidae.

Suborder Menurae.

Suborder Passeres.

b) Members of the pair touch at the ventral midline, not necessarily at insertion.

Cotingidae (part): *Iodopleura, Attila, Casiornis, Laniocera, Rhytipterna, Pachyramphus, Platypsaris.*

Pipridae (part): *Pipra, Chiroxiphia, Corapipo, Manacus, Ilicura.*

Tyrannidae (part): *Agriornis, Xolmis, Muscisaxicola, Lessonia, Neoxolmis, Ochthoeca, Sayornis, Colonia, Gubernetes, Yetapa, Knipolegus, Phaeotriccus, Entotriccus, Lichenops, Muscipipra, Fluvicola, Arundinicola, Pyrocephalus, Muscigralla, Satrapa, Machetornis, Muscivora, Tyrannus, Empidonomus, Megarhynchus, Tyrannopsis, Tolmarchus, Myiarchus* (part), *Nutallornis, Myiochanes, Blacicus, Empidonax, Aechmolophus, Cnemotriccus, Mitrephanes, Pyrrhomyias, Myiophobus, Platyrinchus, Tolmomyias* (part), *Pogonotriccus, Leptotriccus, Phylloscartes, Capsiempis, Euscarthmus, Pseudocolopteryx, Habrura, Tachuris, Stigmatura, Corythopis, Serpophaga, Inezia, Mecocerculus, Colorhamphus, Elaenia, Camptostoma, Phyllomyias, Tyranniscus, Microtriccus, Leptopogon, Mionectes, Pipromorpha.*

Oxyruncidae.

b. M. sternotrachealis.

i. Mode of insertion.

a) Directly on the lateral surface of the trachea.

Eurylaimidae (part): *Cymbirhynchus, Psarisomus, Calyptomena.*

Cotingidae (part) : *Heliochera, Cotinga, Xipholena, Carpodectes, Attila, Casiornis, Lipaugus, Pachyramphus, Perissocephalus.*
Pipridae (part) : *Corapipo, Schiffornis.*
Tyrannidae (part) : *Agriornis, Ochthoeca, Sayornis, Yetapa, Arundinicola, Pyrocephalus, Muscigralla, Satrapa, Legatus, Sirystes, Myiozetetes* (part), *Pitangus, Myiarchus, Eribates, Nuttallornis, Blacicus, Empidonax, Cnemotriccus, Mitrephanes, Terenotriccus, Myiobius, Pyrrhomyias, Myiophobus, Tolmomyias, Rhynchocyclus, Todirostrum, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Pogonotriccus, Leptotriccus, Phylloscartes, Euscarthmus, Tachuris, Spizitornis, Stigmatura, Corythopis, Serpophaga, Mecocerculus, Colorhamphus, Elaenia* (part), *Suiriri, Sublegatus, Phaeomyias, Camptostoma, Tyranniscus, Tyrannulus, Microtriccus, Leptopogon, Pipromorpha.*
Phytotomidae.
Pittidae (part).
Philepittidae.
Acanthisittidae.
Suborder Menurae.
Suborder Passeres.

b) In continuity with M. tracheolateralis.
Eurylaimidae (part) : *Smithornis, Eurylaimus.*
Cotingidae (part) : *Euchlornis, Rhytipterna, Querula, Cephalopterus, Gymnoderus, Conioptilon, Rupicola.*
Pipridae (part) : *Piprites, Chiroxiphia, Manacus.*
Tyrannidae (part) : *Colonia, Onychorhynchus, Oncostoma, Euscarthmornis.*
Pittidae (part).
Oxyruncidae.

c) On the membranous sheath of M. tracheolateralis.
Pipridae (part) : *Pipra.*
Tyrannidae (part) : *Aechmolophus.*

d) By a broad tendinous sheet to the trachea.
Cotingidae (part) : *Pyroderus.*

e) Part of each muscle attached directly to the trachea; the remainder continuous with M. tracheolateralis.
Cotingidae (part) : *Phoenicircus, Iodopleura, Platypsaris.*
Tyrannidae (part) : *Muscipipra, Myiodynastes, Myiozetetes, Pitangus, Nesotriccus, Aphanotriccus, Platyrinchus, Pseudocolopteryx, Elaenia, Leptopogon, Mionectes.*

f) Part of each muscle attached directly to the trachea; the remainder attached to the membranous sheath surrounding M. tracheolateralis.
Pipridae (part) : *Ilicura.*
Tyrannidae (part) : *Xolmis, Neoxolmis, Gubernetes, Lichenops, Empidonomus, Tolmarchus, Myiochanes, Inezia.*

g) Part of each muscle continuous with M. tracheolateralis; the remainder inserting on the membranous sheath surrounding M. tracheolateralis.
Cotingidae (part) : *Laniocera.*

Tyrannidae (part): *Muscisaxicola, Lessonia, Phaeotriccus, Entotriccus.*

h) Three fasciculi: one continuous with M. tracheolateralis; one attached directly to the lateral surface of the trachea; one inserting on the membranous sheath of M. tracheolateralis.
Tyrannidae (part): *Knipolegus, Machetornis, Muscivora, Tyrannus, Megarhynchus, Conopias, Elaenia* (part).

i) By a diffuse tendon to the surface of the intrinsic muscle.
Cotingidae (part): *Procnias.*

2. Intrinsic muscles.
   a. Number present.
      i. None.
         Suborder Eurylaimi.
         Suborder Tyranni (part):
         Cotingidae (part): *Phoenicircus, Heliochera, Cotinga, Xipholena, Carpodectes, Euchlornis, Lipaugus, Tityra, Querula, Pyroderus, Cephalopterus, Perissocephalus, Gymnoderus, Conioptilon, Rupicola.*
         Pipridae (part): *Piprites, Manacus.*
         Tyrannidae (part): *Machetornis, Terenotriccus, Myiobius, Pyrrhomyias, Onychorhynchus, Tyranniscus* (part).
         Phytotomidae.
         Pittidae.
         Philepittidae.
         Acanthisittidae.
      ii. One pair.
         Cotingidae (part): *Iodopleura, Attila, Casiornis, Laniocera, Rhytipterna, Pachyramphus, Platypsaris, Procnias.*
         Pipridae (part): *Pipra, Chiroxiphia, Ilicura, Schiffornis.*
         Tyrannidae (part): all except those with none (above) and those with two pairs (below).
         Oxyruncidae.
      iii. Two pairs.
         Pipridae (part): *Corapipo.*
         Tyrannidae (part): *Ochthoeca, Legatus, Myiozetetes, Nuttallornis, Tolmomyias* (part), *Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Leptotriccus, Phylloscartes, Pseudocolopteryx, Elaenia, Suiriri, Phaeomyias, Camptostoma.*
      iv. Three pairs.
         Suborder Menurae.
      v. Four pairs.
         Suborder Passeres.
   b. Properties of the intrinsic muscles (in birds possessing one pair), or of the ventral intrinsic muscles (in birds possessing two pairs). Properties in birds with three and four pairs are not handled in this summary.
      i. Region of origin.
         a) Adjacent to the ventral midline or by a raphe (indicated by "r") to the ventral midline, or both.
         Cotingidae (part): *Iodopleura.*

Tyrannidae (part): *Sayornis* (r), *Knipolegus, Phaeotriccus, Arundinicola* (r), *Muscigralla* (r), *Legatus, Myiozetetes, Nesotriccus, Nuttallornis* (r), *Myiochanes* (r), *Blacicus* (r), *Empidonax* (r), *Aechmolophus* (r), *Aphanotriccus* (r), *Rhynchocyclus* (r), *Pogonotriccus* (r), *Leptotriccus, Euscarthmus* (r), *Pseudocolopteryx* (r), *Stigmatura* (r), *Corythopis* (r), *Inezia* (r), *Elaenia* (part, r), *Suiriri* (r), *Phaeomyias* (r), *Camptostoma, Phyllomyias, Tyranniscus* (part), *Microtriccus, Leptopogon.*
Oxyruncidae.

b) Adjacent to the ventral midline and on the ventral and ventrilateral surfaces of one or more elements.
Cotingidae (part): *Attila, Casiornis, Laniocera, Rhytipterna.*
Pipridae (part): *Ilicura.*
Tyrannidae (part): *Agriornis, Xolmis, Neoxolmis, Entotriccus, Fluvicola, Sirystes, Myiarchus, Eribates, Capsiempis, Elaenia* (part).

c) Directly on the ventral region of one or more elements.
Tyrannidae (part): *Pyrocephalus* (part), *Platyrinchus, Oncostoma, Hemitriccus, Tachuris, Colorhamphus, Mionectes, Pipromorpha.*

d) Directly on the ventral and ventrilateral surfaces of one or more elements.
Pipridae (part): *Pipra, Chiroxiphia.*
Tyrannidae (part): *Lessonia, Ochthoeca, Pyrocephalus* (part), *Tolmomyias, Oncostoma, Euscarthmornis, Colopteryx, Myiornis, Phylloscartes, Spizitornis.*

e) Directly on the ventrilateral surfaces of one or more elements.
Cotingidae (part): *Pachyramphus, Platypsaris.*

f) Directly on the ventrilateral, lateral and dorsolateral surfaces of one or more elements.
Tyrannidae (part): *Tyrannus, Empidonomus, Myiodynastes, Conopias, Tyrannopsis, Tolmarchus.*

g) Directly on the ventral, ventrilateral and lateral surfaces of one or more elements.
Tyrannidae (part): *Gubernetes, Yetapa, Muscivora, Pitangus, Habrura, Serpophaga, Mecocerculus.*

h) Directly on the lateral surfaces of one or more elements.
Pipridae (part): *Corapipo, Schiffornis.*
Tyrannidae (part): *Tolmomyias* (part), *Todirostrum.*

i) Adjacent to the ventral midline and along the ventral, ventrilateral and lateral surfaces of one or more elements.
Tyrannidae (part): *Colonia, Cnemotriccus, Tyrannulus.*

j) Adjacent to the ventral midline (or by a raphe to the midline) and on the ventral, ventrilateral, lateral and dorsolateral surfaces of one or more elements.
Tyrannidae (part): *Lichenops, Pitangus* (part), *Myiophobus.*

k) Completely encircling the trachea on several elements.
Cotingidae (part): *Procnias.*

ii. Element and region of insertion.

a) A-1, dorsal 1/5th of the element.
Tyrannidae (part): *Myiozetetes, Platyrinchus.*

b) A-1, middle region (1/5 - 1/3 the length of the element).
Tyrannidae (part): *Agriornis, Xolmis, Colonia, Gubernetes, Knipolegus, Entotriccus, Muscipipra, Fluvicola, Satrapa, Sirystes, Myiarchus, Eribates, Nuttallornis, Myiochanes, Empidonax, Mitrephanes, Rhynchocyclus, Tolmomyias.*

c) A-1, ventral end, terminally.
Pipridae (part): *Corapipo.*

d) A-1, ventral 1/3 - 1/2.
Cotingidae (part): *Casiornis, Rhytipterna.*
Tyrannidae (part): *Muscisaxicola, Lessonia, Ochthoeca, Phaeotriccus, Muscigralla, Blacicus, Aechmolophus, Pseudocolopteryx, Elaenia* (part).

e) A-1, ventral 2/3.
Tyrannidae (part): *Neoxolmis, Sayornis, Aphanotriccus.*

f) A-1/B-1 membrane.
Cotingidae (part): *Attila, Laniocera.*
Tyrannidae (part): *Yetapa, Arundinicola, Pyrocephalus, Cnemotriccus, Leptotriccus, Phylloscartes, Habrura, Spizitornis, Stigmatura, Corythopis, Elaenia* (part), *Phyllomyias, Tyrannulus.*

g) B-1, dorsal 1/5.
Cotingidae (part): *Iodopleura, Platypsaris.*
Tyrannidae (part): *Empidonomus, Legatus, Conopias, Pitangus* (part), *Platyrinchus, Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Pogonotriccus, Inezia, Elaenia, Suiriri, Phaeomyias, Camptostoma, Tyranniscus* (part), *Microtriccus, Leptopogon.*

h) B-1, center.
Cotingidae (part): *Pachyramphus.*
Pipridae (part): *Schiffornis.*
Tyrannidae (part): *Tolmomyias, Todirostrum, Euscarthmus, Tachuris, Colorhamphus.*
Oxyruncidae.

i) B-1, ventral 1/6.
Tyrannidae (part): *Mionectes.*

j) B-1, entire length.
Pipridae (part): *Ilicura.*

k) B-1/B-2 membrane, dorsolateral region.
Tyrannidae (part): *Tolmarchus.*

l) On more than one element and/or membrane.
A-1 and B-1, dorsolaterally. Tyrannidae: *Muscivora, Nesotriccus, Myiophobus.*
A-1 and B-1, ventrilaterally. Tyrannidae: *Pipromorpha.*
A-1/B-1 membrane and B-1, laterally. Tyrannidae: *Serpophaga.*
A-1, B-1, and B-1/B-2 membrane. Tyrannidae: *Tyrannus.*
A-1/A-2 membrane, A-1, B-1, and B-1/B-2 membrane, dorsolaterally. Tyrannidae: *Myiodynastes.*
A-1, A-1/B-1 membrane, B-1/B-2 membrane, and B-2, dorsolaterally. Tyrannidae: *Megarhynchus, Pitangus* (part).

A-1/B-1 membrane, B-1, B-1/B-2 membrane, B-2, nearly the entire areas of these elements; anterior edges of the internal tympaniform membranes. Cotingidae: *Procnias.*

- iii. Fiber direction.
  - a) Approximately parallel to the bronchial axis.
    Cotingidae (part) : *Procnias.*
    Pipridae (part) : *Pipra, Chiroxiphia, Schiffornis.*
    Tyrannidae (part): *Tolmomyias* (part), *Todirostrum, Spizitornis, Mecocerculus.*
  - b) Ventral fibers oblique; lateral or dorsal ones approximately parallel to the bronchial axis.
    Cotingidae (part) : *Attila, Casiornis, Laniocera, Rhytipterna.*
    Tyrannidae (part): *Agriornis, Xolmis, Muscisaxicola, Lessonia, Neoxolmis, Ochthoeca, Colonia, Gubernetes, Yetapa, Knipolegus, Entotriccus, Lichenops, Muscipipra, Fluvicola, Pyrocephalus* (part), *Satrapa, Muscivora, Tyrannus, Empidonomus, Legatus, Sirystes, Myiodynastes, Megarhynchus, Conopias, Pitangus, Myiozetetes, Tolmarchus, Myiarchus, Eribates, Nesotriccus, Cnemotriccus, Myiophobus, Tolmomyias* (part), *Capsiempis, Habrura, Serpophaga, Elaenia* (part), *Tyrannulus.*
  - c) All fibers oblique (anteroventrimedial-posterodorsolateral).
    Cotingidae (part) : *Iodopleura, Pachyramphus, Platypsaris.*
    Pipridae (part) : *Ilicura.*
    Tyrannidae (part) : *Sayornis, Phaeotriccus, Arundinicola, Pyrocephalus* (part), *Muscigralla, Nuttallornis, Myiochanes, Blacicus, Empidonax, Aechmolophus, Mitrephanes, Aphanotriccus, Platyrinchus, Rhynchocyclus, Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Pogonotriccus, Leptotriccus, Phylloscartes, Euscarthmus, Pseudocolopteryx, Tachuris, Stigmatura, Corythopis, Inezia, Colorhamphus, Elaenia* (part), *Suiriri, Sublegatus, Phaeomyias, Camptostoma, Tyranniscus* (part), *Microtriccus, Leptopogon, Mionectes, Pipromorpha.*
    Oxyruncidae.

c. Properties of the lateral or dorsal intrinsic muscle, in birds possessing two pairs.

- i. Region of origin.
  - a) On the lateral surface of one or more elements.
    Pipridae (part) : *Corapipo.*
    Tyrannidae (part) : *Legatus, Myiozetetes, Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Leptotriccus, Phylloscartes, Pseudocolopteryx.*
  - b) On the dorsolateral surface of one or more elements.
    Tyrannidae (part): *Nuttallornis, Tolmomyias* (part), *Hemitriccus, Elaenia, Suiriri, Phaeomyias, Camptostoma.*
  - c) Near the dorsal midline of two or more elements.
    Tyrannidae (part) : *Ochthoeca.*
- ii. Element and region of insertion.
  - a) A-1, dorsal end.
    Pipridae (part) : *Corapipo.*

b) A-1, center.
Tyrannidae (part): *Ochthoeca, Nuttallornis, Tolmomyias, Pseudocolopteryx, Elaenia* (part), *Suiriri, Phaeomyias.*

c) A-1, ventral 1/3.
Tyrannidae (part): *Elaenia* (part).

d) A-1/B-1 membrane, center.
Tyrannidae (part): *Phylloscartes, Leptotriccus.*

e) B-1, dorsal end.
Tyrannidae (part): *Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus.*

f) B-1, center.
Tyrannidae (part): *Camptostoma.*

g) B-1, ventral 1/2.
Tyrannidae (part): *Legatus, Myiozetetes.*

MAJOR STRUCTURAL DIVISIONS.

The preceding detailed morphological summary does not fully express the broad structural groups into which passerine syringes may be divided. The following groups comprise birds whose syringes share a number of features not found in other groups. To these features are added others that characterize the group, but are shared with some other groups. The outline is not presented as a taxonomic classification: it merely reflects the different levels of structural complexity found in the passerine syrinx.

Division I

Limited modification of tracheobronchial region. Little or no fusion of A-elements. Pessulus present. No internal cartilages. Mm. tracheolaterales usually narrow or medium in width; insert on divided or double A-element. Mm. sternotracheales usually narrow, insertion variable. No intrinsic muscles. Some groups placed in this division do not conform with above in certain characteristics, but are placed here because of general conformity.

Suborder Eurylaimi.
  Eurylaimidae. (Mm. tracheolaterales insert on a complete element in *Smithornis.*)
Suborder Tyranni.
  Superfamily Tyrannoidea.
    Cotingidae (part): all except *Attila, Casiornis, Rhytipterna, Procnias, Laniocera, Pachyramphus, Platypsaris, Iodopleura.*
    Pipridae (part): *Piprites.*
    Tyrannidae (part): *Terenotriccus, Myiobius, Pyrrhomyias, Onychorhynchus.* (Internal cartilages present in *Myiobius.*)
    Phytotomidae.
    Pittidae (pessulus lacking in most species).
    Philepittidae (internal cartilages present in *Neodrepanis*).
    Acanthisittidae. Much fusion of A-elements; Mm. tracheolaterales insert on a complete element; internal cartilages present in *Acanthisitta.*

Division II

Lower trachea dorsoventrally compressed; elements in compressed region attenuated and sometimes lacking, compressed region thus forming "windows" (Membranae tracheales). Fusion of A-elements, when present, always anterior to Membranae. Lateral bars or plates (Processi vocales) present. Pessulus invariably lacking. Mm. tracheolaterales variable, inserting either on Processi, on elements anterior to Membranae, or both. Mm. sternotracheales insert on anterior ends of Processi and/or on elements anterior to Membranae. Intrinsic muscles consist of none, one, or two pairs; if present, they originate on elements anterior to Membranae and insert on Processi (rarely, also on elements posterior to Membranae).

Suborder Tyranni.

Superfamily Furnarioidea.

Subdivision A.

Processi large, straight, thick bars. No intrinsic muscles.

Formicariidae (part): *Formicarius, Chamaeza, Grallaria, Conopophaga.*

Rhinocryptidae (part): *Teledromas.*

Subdivision B.

Processi small soft plates anchored to underlying elements by strong fibrous sheets. Each M. sternotrachealis inserts by two fasciculi, one to Processus, other to dorsolateral surfaces of several elements immediately anterior to Membranae. One pair of intrinsic muscles present (Mm. vocales ventrales); originates near ventral midline and/or ventrilateral surfaces of several elements immediately anterior to Membranae; insert on anterodorsal regions of Processi.

Formicariidae (part): all except *Formicarius, Chamaeza, Grallaria* and *Conopophaga.*

Subdivision C.

Processi nearly straight, broad at ends and narrow in middle. Mm. sternotracheales insert on flared anterior ends of Processi. One pair of intrinsic muscles present (Mm. vocales dorsales); originates laterally on elements immediately anterior to Membranae; inserts on anteroventral or ventral regions of Processi.

Rhinocryptidae (part): all except *Teledromas.*

Subdivision D.

Processi nearly straight, usually broad at ends and narrow in middle (as in Subdivision C.); rarely of uniform width. Insertion of Mm. tracheolaterales several elements removed from Membranae tracheales. Mm. sternotracheales insert on anterior ends of Processi. Two pairs of intrinsic muscles present (Mm. vocales ventrales and Mm. vocales dorsales); originate on anterior edge of drum; insert on Processi.

Furnariidae (part): all except *Geositta.*

Subdivision E.

Processi broad at bases; prominent "horns" extend from middle of dorsal and ventral sides. Fusion of two or more A-elements usually present, always including one immediately anterior to Membranae. Mm. tracheolaterales insert on anterior edge of drum thus formed. Mm. sternotracheales as in Subdivision D, above. Two pairs of intrinsic muscles present (Mm. vocales ventrales and Mm. vocales dorsales); originate as in Subdivision D; insert on ventral and dorsal "horns" of Processi, respectively.

Dendrocolaptidae.

Furnariidae (part): *Geositta.*

Division III

Lower trachea roughly cylindrical, with or without fusion of A-elements. Pessulus present or absent. Internal cartilages present (except in Subdivision A). Mm. tracheolaterales frequently, but not always, in contact with each other at ventral midline; usually insert on one or more A-elements at level of A-4 or above. Mm. sternotracheales variable in type of insertion. When two pairs of intrinsic muscles are present, Mm. sternotracheales usually insert dorsal or anterodorsal to origins of both. Intrinsic muscles number one or two pairs. Within this division several subdivisions are recognized, but not all members of the division are included in them, as morphological variation is complex and frequently clinal.

Suborder Tyranni
  Superfamily Tyrannoidea
    Cotingidae (part): *Attila, Laniocera, Platypsaris, Iodopleura, Casiornis, Rhytipterna, Pachyramphus.*
    Pipridae (part): *Pipra, Chiroxiphia, Corapipo, Schiffornis.*
    Tyrannidae (part): all except *Machetornis, Terenotriccus, Myiobius, Pyrrhomyias, Onychorhynchus.*

Subdivision A.

Internal cartilages absent. Pessulus present. Rigid cylindrical drum formed of fused A-elements. One pair of intrinsic muscles.

Pipridae (part): *Pipra, Chiroxiphia.*

Subdivision B.

Fusion, when present, involves only two or three A-elements. Pessulus present or absent. Two pairs of internal cartilages present, dorsal and larger pair J- or ⅃-shaped. One pair of intrinsic muscles (Mm. obliqui ventrales).

Cotingidae (part): *Attila, Casiornis, Rhytipterna, Laniocera.*

Tyrannidae (part): *Myiarchus, Eribates.*

Subdivision C.

Fusion, when present, incomplete (except in *Empidonomus*), but lower four or five A-elements always closely fitted. A-2 double. A-2, A-3, and sometimes A-4 with sharp corners in dorsomedial region. B-1 and B-2 fused at their ventral ends (except in *Pitangus,* in which B-3 and B-4 are fused). Pessulus present or absent (sometimes both in same genus). Internal cartilages straight or J-shaped. Mm. sternotracheales thick, usually with multiple insertions. One pair of intrinsic muscles (Mm. obliqui ventrales); short, broad and extremely thick, not touching at ventral midline; originating on ventrilateral, lateral and dorsolateral surfaces of several elements; having multiple dorsolateral insertion.

Tyrannidae (part): *Muscivora, Tyrannus, Empidonomus, Tyrannopsis, Myiodynastes, Megarhynchus, Conopias, Tolmarchus, Pitangus.*

Subdivision D.

Little or no fusion of elements, but divided A-elements usually closely fitted. Lower three or four A-elements divided. Pessulus present or absent; when present, free at one end. Cartilaginous plug or transverse bridge in dorsal interbronchial region. Internal cartilages short rounded triangles or straight bars, fused to cartilaginous plug. Mm. tracheolaterales extend under intrinsic muscles to insert on A-1 and/or A-2. Mm. sternotracheales insert directly on trachea (except in *Myiochanes*). One pair of intrinsic muscles present, except in *Nuttallornis,* which has two pairs. Mm. obliqui ventrales originate on midventral raphe (except in some specimens of *Sayornis,* in which pair of muscles are ventrally continuous) and insert on A-1.

Tyrannidae (part): *Sayornis, Nuttallornis, Myiochanes* [= *Contopus*], *Blacicus, Empidonax, Aphanotriccus, Mitrephanes.*

Subdivision E.

Three or more A-elements fused, completely or partially, into rigid drum. Pessulus present and fused to drum. Internal cartilages consist of narrow straight or curved bars bearing thin semicircular ventral extensions (except in *Suiriri* and *Phaeomyias*). Mm. sternotracheales insert directly (rarely, also with continuity with Mm. tracheolaterales). Two pairs of intrinsic muscles present (except in *Microtriccus*). Ventral pair (Mm. obliqui ventrales) originates on a midventral raphe which is attached to drum; insert directly on A-1 or on A-1/B-1 membrane, or by a tendon to dorsal fifth of B-1. Lateral pair (Mm. obliqui laterales) originates ventrilaterally and laterally and inserts directly on A-1.

Tyrannidae (part): *Elaenia, Suiriri, Phaeomyias, Camptostoma, Microtriccus.*

Subdivision F.

Lower trachea characterized by the presence of many dorsally incomplete elements, each with a rather wide opening at the dorsal midline. Pessulus present; bends anteriad at dorsal surface of syrinx, extending up dorsal midline in openings of dorsally incomplete elements. Mm. sternotracheales thick, insertion variable. Two pairs of intrinsic muscles usually present. Ventral pair (Mm. obliqui ventrales) originate ventrally and interdigitate at origin; insert subterminally on dorsal end of B-1. Lateral pair (Mm. obliqui laterales) originates immediately posterior to the insertion of Mm. sternotracheales and inserts dorsally adjacent to Mm. obliqui ventrales.

Tyrannidae (part): *Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus.*

Division IV

Lower three A-elements divided, consisting of thick round bars, slightly curved and flattened at dorsal ends. Pessulus present (except in the Alaudidae) and fused to A-4 at both ends. No internal cartilages. Mm. tracheolaterales insert on the anterior surface of the syringeal aponeurosis and on the lateral, dorsolateral and dorsal surfaces of the trachea. Mm. sternotracheales insert on the lateral surface of the trachea, posterior to syringeal aponeurosis and between the dorsal and ventral long intrinsic muscles. Three or four pairs of intrinsic muscles present, always including one pair of ventral long muscles (Mm. bronchotracheales antici) and one pair of dorsal long muscles (Mm. bronchotracheales postici); originate on the posterior surface of syringeal aponeurosis and on lateral and dorsolateral surfaces of the trachea; insert on respective ends of A-1 and A-2.

Suborder Menurae.

Suborder Passeres

Subdivision A.

No fusion of A-elements. Three pairs of intrinsic muscles present, ventral and dorsal pairs of long muscles and pair of short dorsal muscles.

Suborder Menurae.

Subdivision B.

Elements A-4 through A-7 (rarely, through A-8) fused, forming drum. Four pairs of intrinsic muscles present, those found in Subdivision A. and pair of short ventral muscles.

Suborder Passeres (Pessulus lacking in Alaudidae).

HISTORY OF PASSERINE CLASSIFICATION

In the eighteenth century the order Passeriformes was considered to include virtually all terrestrial and arboreal birds except the birds of prey, the game birds, and the large cursorial forms. The increase of anatomical knowledge in the nineteenth century resulted in the gradual narrowing of the order to its modern limits.

Nitzsch (1829, 1840), basing his conclusions on the anatomy of the carotid arteries, pterylosis, and syrinx, separated several other orders from the passerines. Sundevall (1872) pointed out that certain families, which include only the hoopoes (Upupidae) and most of the modern Passeriformes, lack the connecting vinculum between certain tendons of the leg M. flexor halucis longus and M. flexor perforans digitorum. Keyserling and Blasius (1839) observed that all passerines in which the syrinx is elaborately muscled (i.e., the oscines) possess bilaminate planta tarsi. Müller (1847) viewed the passerines in the broad sense and his contribution was to the subdivisions of the order, rather than to its boundaries.

Cabanis and Heine (1859) treated the Passeriformes with essentially the same classification as is used today, combining the ideas of Nitzsch, Keyserling and Blasius, and Müller. Lacking knowledge of the internal anatomy of many forms, Cabanis and Heine were sometimes misled by external appearances. They included the pittas with some of the antbirds in their Hypocnemidae, the lyrebirds (*Menura*) with the tapaculos (Rhinocryptidae), and the nonpasserine todies (Coraciiformes) with the Tyrannidae. Their family mergers—the modern Furnariidae and Dendrocolaptidae in a single family Anabatinae and the modern Cotingidae and Pipridae in a family Ampelidae—were endorsed by many subsequent authors. Their arrangement of genera in the tyrant flycatchers, cotingas, and manakins formed the basis for the later arrangements of Sclater (1888), von Berlepsch (1905) and Hellmayr (1927).

More than any other man, A. H. Garrod was responsible for the modern boundaries and subdivisions of the Passeriformes. He defined the order (1873, 1876) in terms of the short colic caeca, nude oil gland, aegithognathous palate, the absence of M. ambiens in the knee, and the form of the tendon of M. tensor patagi brevis. He separated the broadbills (Eurylaimidae) from the rest of the order on the basis of their plantar vinculum and non-bifurcate Manubrium sterni [= *Spina sternalis*]. On the basis of syringeal muscle attachments, he divided the remaining passerines into Acromyodae and Mesomyodi. The former were further divided into "Normales" (oscines) and "Abnormales" (Menurae) depending on the number of syringeal muscles. He divided the Mesomyodae, which were synonymous with the modern suborder Tyranni, into Tracheophonae (the superfamily Furnarioidea) and Oligomyodae (Tyrannoidea) on the Müllerian basis. Within his Tracheophonae he separated the Furnariidae from the Dendrocolaptidae on the basis of nasal osteology. Garrod also attempted, with some success, to separate the Pipridae and Cotingidae (except *Rupicola*) from the other Tyrannoidea on the basis of the dominant artery of the thigh. He removed the pittas from the antbirds after a study of the syrinx and skull and placed them in his Oligomyodae.

After Garrod's death in 1879, his work was continued by his student, W. A. Forbes, who studied several genera about which little was known. On the basis of syrinx, tarsal scutellation, and the osteology of the sternum and nasal bones, he established the family Conopophagidae (1881) for the genera *Conopophaga* and *Corythopis*. The family was subsequently submerged by Ames, Heimerdinger and Warter (1968). The New Zealand "wrens," *Xenicus* and *Acanthisitta,* were removed from the oscines by Forbes (1882a) and placed in the Oligomyodae as the family Xenicidae (now Acanthisittidae). He defined the Philepittidae (1880b) on the basis of their syringeal structure, non-bifurcate Manubrium sterni, and lack of a plantar vinculum. By 1885 the relationships and limits of all the non-oscine families were understood essentially as they are today.

P.L. Sclater (1888) accepted most of the ideas of Garrod and Forbes, but separated the broadbills at a lower level of the system. His first and second divisions of the order were based on syringeal structure. The Acromyodi and Mesomyodi were the same as in Garrod's classification, except that the Eurylaimidae were included in the Mesomyodi. The Mesomyodi were divided into Oligomyodi and Tracheophonae, as was done by Garrod. Sclater further divided the Oligomyodi on the basis of the plantar tendons, placing the broadbills in the Desmodactyli and the rest, comprising the modern Tyrannoidea, in the Eleutherodactyli. Sclater relied on tarsal scutellation, the degree of syndactyly, and bill shape to define the eight families of his Eleutherodactyli. Four subfamilies of the Tyrannidae were based on the proportions of the legs and feet, on habitat and coloration, and on the degree of development of rictal bristles.

Hans Gadow (in Gadow and Selenka, 1893) relied heavily on the syrinx in classifying the Passeriformes. One half of the order, designated "Anisomyodae" because the syringeal muscles were thought to be dorsoventrally asymmetrical, included the Subclamatores (Eurylaimidae) and Clamatores (Pittidae, Xenicidae, Tyrannidae, Formicariidae, and Pteroptochidae). In the Tyrannidae were two subfamilies: Tyranninae (including the manakins) and Cotinginae. The Conopophigidae of other authors were included by Gadow in the Formicariidae; the Furnariidae and Dendrocolaptidae were in his Pteroptochidae. The other half of the Passeriformes, which he called "Diacromyodae" because the syringeal muscles are attached to both ends of the elements, contained the "Suboscines" (*Menura*) and Oscines.

Ridgway (1901-1907) divided the Passeriformes into two suborders on the basis of the plantar vinculum. The Eurylaimi alone constituted his Desmodactyli, all other groups being in the Eleutherodactyli. In the latter suborder he recognized three superfamilies: Clamatores (Tyranni), Pseudoscines (Menurae), and Oscines. The Clamatores were divided into Tracheophonae and Oligomyodae, as they were by Garrod. Ridgway relied strongly on the type of tarsal scutellation to determine family boundaries, often contrary to his better judgment.

Pycraft (in Ridgway, 1907, part IV, p. 332) differed from most of his contemporaries in his arrangement of the passerines. He recognized four suborders, based largely on syringeal structure. One of these contained the Eurylaimidae, Cotingidae and Philepittidae, another the "Tracheophonae" (Furnariodea), a third the Tyrannidae (and presumably the Pipridae) and Pittidae, the fourth "the rest of the passeres." The tracheophonae were divided into three subgroups based on the nasal bones and the number of notches in the metasternum.

Von Ihering (1904) attempted to subdivide the Tyrannidae on a non-morphological basis, using primarily the form of the nest, egg color, and zoogeography. He altered the subfamilies employed by Sclater, splitting some and merging others. Moreover, he speculated that the common ancestor of the tyrant flycatchers and manakins was a small olive bird with a "somewhat compressed and bristled bill and pronounced syndactyly," like certain of the modern Elaeniinae. Although he dealt with only about a third of the Tyrannidae, von Ihering introduced new taxonomic criteria in a family in which feeding adaptations had been overemphasized as taxonomic characters. His ideas had a profound effect on subsequent classifiers, particularly von Berlepsch and Hellmayr.

Von Berlepsch (1905) attempted to arrange the Tyrannidae "according to their natural relationships." Although he followed many of von Ihering's suggestions, he relied principally on external structural characters and on intuition.

Hellmayr (1924-38) produced the most recent complete revision of the New World passerines. He followed Garrod's classification with regard to major subdivisions, but employed non-anatomical names for the subdivisions. He recognized two suborders in the Western Hemisphere passerines: the Tyranni (equivalent to Garrod's Mesomyodi) and Passeres (Acromyodi normales). The two superfamilies of the Tyranni, the Furnarioidea and Tyrannoidea, were precisely equivalent to the Tracheophonae and Oligomyodi as far as the included families were concerned. Hellmayr disagreed with Sclater and with Ridgway on the systematic positions of many genera. Where Ridgway attempted to adhere to rigid structural criteria, Hellmayr was more flexible. Nevertheless, he regarded Ridgway's opinions highly and the family allocations of many genera show Ridgway's reliance on tarsal scutellation, rather than Hellmayr's intuition. In arranging the Tyrannidae and Pipridae he used beak shape, wing shape and tarsal scutellation, in conjunction with an assortment of other characters, to establish intergeneric relationships.

Peters (1951) and Wetmore (1960) agreed with Hellmayr on the subordinal divisions of the Passeriformes. Their classification of the order was the result of more than a century of accumulated anatomical and behavioral investigation by scores of ornithologists. Despite this large amount of knowledge there are many unsolved questions in passerine systematics. The allocation of the three Old World families of ground dwelling birds, Pittidae, Philepittidae, and Acanthisittidae, to the Tyranni is based on scanty evidence. The family boundaries of the Tyrannidae, Pipridae, and Cotingidae are greatly in need of reëvaluation, for no one has examined the taxonomic characters of these groups since Ridgway (1907).

Inasmuch as the major subdivisions of the Passeriformes, as presently understood, are based on syringeal morphology, it is singularly appropriate to examine the classification of the order in the light of the data of the present investigation.

COMMENTS ON THE ADJECTIVES OF SYRINGEAL MORPHOLOGY

INTRODUCTION.

Throughout the history of syringeal study anatomists have named the parts of the syrinx on the basis of assumed function or of similarity to the respiratory systems of other animals. A re-examination of the classical adjectives now appears warranted, with particular attention to the series of "-myodean" words introduced by Müller, Huxley, and others, and to the terms "tracheal" and "bronchial."

THE "-MYODEAN" ADJECTIVES.

Of the eight terms ending in "-myodean" two, "polymyodean" and "oligomyodean," refer to the number of intrinsic muscles, the others to the position of their insertion. Müller (1847) applied the term "Passerini Polymyodi" to the birds with complex syringes (oscines), but stated that the term was only descriptive, not intended to denote a taxonomic division of the order. Huxley (1867) used the term "oligomyodi" to designate those passerines treated by Müller as "Picarii." In their original sense the two words served to describe in approximate terms two of the syringeal types on which the separation of the oscines from the other passerines was based. The polymyodean syrinx has four or five pairs of intrinsic muscles, according to Müller. More important, they act on the ends of two or more cartilaginous elements. Multiplicity of action was stressed more strongly by Müller than the number of muscles. He placed *Menura,* which he believed to have only two pairs of intrinsic muscles, in the "Polymyodi" group because the insertions of the muscles are widely separated dorsoventrally. In the Müllerian sense, the terms "polymyodean" and "oligomyodean" are not wholly appropriate, being names based on muscle numbers, but employed on the basis of muscle attachments. Subsequent use of the terms as taxonomic names (Sclater, 1888; Ridgway, 1901-1907) was even less appropriate, for only a few of the birds involved had been studied anatomically.

Recognizing the weakness in the application of poly- and oligomyodean, Garrod (1876) coined two new words intended to describe more accurately the conditions present. He referred to the condition found in Müller's "Polymyodi" as "acromyodean," and to that in Müller's "Picari" (the Oligomyodi of Huxley) as "mesomyodean." In Garrod's outline of passerine classification the "Mesomyodi" and "Acromyodi" were the first subdivisions of the order. Garrod included in his Mesomyodi the groups placed by Müller in the third major division, Tracheophones.

Gadow and Selenka (1893) introduced more detailed modifications of "acromyodean": the words "anisomyodean" and "an-," "cat-," and "diacromyodean." They defined various types of musculature in terms of dorsoventral symmetry, or lack of it, and of the point of insertion. Although the words are valid for describing many syringeal types, they are inadequate to describe the broad array of muscle forms found in the Tyrannoidea. In most applications the specialized positional terms of Garrod and of Gadow and Selenka oversimplify the actual situations, creating false impressions about similarities.

THE TERMS "TRACHEAL" AND "BRONCHIAL".

Included in the description of the anatomy of a species one often finds the statement that the syrinx is "tracheo-bronchial" or "tracheal." The application of these terms is based on the assumption that the trachea or the bronchi may be distinguished by the nature of the lumen or of the supporting elements. At some finite point in each individual the lumen of the trachea divides to form the bronchi, but the precise location of the point of divergence is highly variable. The point of change from one passage to two is not always where the elements cease to be complete rings.

Miller (1934) suggested using the position of the pessulus or the point of insertion of syringeal muscles as reference points for syringeal comparisons. In his study of owl vocal mechanisms he used the pessulus as a base point. For comparisons among the Strigidae the pessulus offers a stable point, but in the suboscine passerines the position of the pessulus does not show clear relationship to muscles and other cartilages. Moreover the presence or absence of the pessulus shows individual variation in at least one species (*Tyrannus tyrannus*).

Throughout the nineteenth century the reference point in syringeal descriptions was the so-called "tracheo-bronchial" junction, the point at which one can say that anterior ("tracheal") elements are complete and posterior ("bronchial") ones divided or double. Difficulty arises in designating as tracheal or bronchial those elements which are incomplete dorsally or ventrally; usually they have been called tracheal.

Some authors have recognized that divided elements are not always uniform. Garrod (1877a) noted the similarity of the anterior divided elements of pittas to the obviously tracheal complete elements. Lowe (1942) suggested that the four flattened "bronchial rings" (A-1 through A-4) of *Manacus vitellinus* might, "in fact, be tracheal derivates." In this case, he concluded, the syrinx of *Manacus* would be "tracheophone." Evolutionarily all divided A-elements may be derived from complete ones, but embryologically they are probably never complete, judging from *Sayornis* and *Fluvicola*. The words "tracheal" and "bronchial," usually associated with the gross configurations of the air passages, do not lend themselves to descriptions of the supporting cartilages, which vary with greater complexity than do the passages.

Designation of the entire syrinx as tracheal or tracheo-bronchial depends on understanding the functions of syringeal components. Assumptions regarding the functions of certain parts of the syrinx sometimes have been made with little evidence. Müller (1847) named the group of birds which possess Membranae tracheales the "Tracheophones," a term used by many subsequent authors. Implicit in the name is the assumption that the Membranae tracheales are the primary source of sound vibrations. Available evidence indiciates that in this type of syrinx, as in most other types, at least some vibrations are produced by the internal tympaniform membranes (Ruppell, 1933). Members of the furnariid genus *Synallaxis* appear to lack the Membranae tracheales at hatching, yet the nestlings are quite vocal (Dorst, 1963). The sounds of the young are quite different from those of the adults, but the differences may well be due to size effects or to the development of controls, rather than to the use of a different part of the syrinx. If the tympaniform membranes are a source of sound, the ovenbirds and their relatives must be said to have a "tracheo-bronchial" syrinx, as do all other passerines.

In short, it is meaningless to apply positional terms to the syrinx and to use them as taxonomic characters without an understanding of syringeal mechanics, or without carefully defining the structural limits of the syrinx. The use of the adjectives "tracheal" and "tracheo-bronchial," particularly, requires the definition of element types, as well as the criteria for deciding what constitutes the syrinx. The latter question hinges on the role of the internal tympaniform membranes and of the extrinsic muscles.

THE EVOLUTION OF THE SYRINX

THE PRIMITIVE CONDITION.

It is widely accepted that the woodpeckers and allies (Order Piciformes) are the nearest living relatives of the Passeriformes. Similarities in the colic caeca, carotid arteries, leg muscle formulae and certain tendons of the wing were summarized by Garrod (1876). The rollers and allies (Coraciiformes) also are believed to be closely related to the Passeriformes, on the basis of their nude oil gland, heterodactyl foot, and general appearance. In both the Piciformes and the Coraciiformes the syrinx is a slightly modified tracheo-bronchial junction (Beddard, 1898) in which some elements may be fused into a drum and the pessulus is usually, but not always, present. There is only a single narrow lateral muscle, which I have found to be M. tracheolateralis in the few specimens of these orders examined (*Piculus, Colaptes* and *Dendrocopus* in the Piciformes; *Eumomota, Electron* and *Todus* in the Coraciiformes). Beddard referred to "intrinsic" muscles in his descriptions of some piciform and coraciiform syringes, but he described only the insertions, and it appears from his illustrations that this "intrinsic" muscle is M. tracheolateralis in all cases. The only other syringeal muscle in members of these two orders is M. sternotrachealis, which usually inserts in continuity with M. tracheolateralis. This syringeal pattern, with only slight modifications, is found in a large number of avian orders. It is likely that this type of syrinx, widely distributed in modern non-passerines, was present in the stock ancestral to the Passeriformes, Piciformes, and probably Coraciiformes. In the following discussion I will consider it primitive and will refer to it as the "pico-passerine" type. In summary, the characters of the pico-passerine syrinx are: 1) simple tracheobronchial junction, with or without fusion, and without accessory cartilages; 2) pessulus present; 3) intrinsic muscles lacking; 4) M. tracheolateralis narrow and laterally situated; 5) M. sternotrachealis inserting laterally and usually in continuity with M. tracheolateralis.

Among the recent passerines, syringes of the pico-passerine type are found in the Eurylaimidae, Philepittidae, Pittidae, Phytotomidae, and Acanthisittidae, and in some members of the Tyrannidae, Cotingidae and Pipridae. There is no evidence in the present simple syrinx of these birds to show that it did not evolve from a more elaborate one, but one might expect some vestige of the more complex condition to remain. The presence of the drum in the Acanthisittidae suggests that the ancestors of this group might have possessed intrinsic muscles (usually found in association with fusion of lower A-elements), but the drum may have some other function than providing a stable base for the intrinsic muscles.

FUNCTIONAL CONSIDERATIONS.

Any discussion of evolutionary changes is clarified if the direct functional significance of those changes is understood. Unfortunately there is little experimental evidence relating to the mechanics of the syrinx, most theories of syringeal operation being based on anatomy and on acoustic analysis. In one of the few *in vitro* studies to date, Rüppell (1933) showed that in non-passerines the internal tympaniform membranes are the primary source of sound vibrations. Miskimen (1951) demonstrated that the same membranes are also the primary source of sound in the songbirds ("oscines") and that the semilunar membrane is relatively unimportant.

Greenewalt (1968) studied the vocalizations of a number of passerine and non-passerine birds, in the most thorough analysis of the acoustic basis of bird song yet done. He divided vocalizations into two basic "domains," whistled and harmonic. In the former the sound is virtually sinusoidal and nearly all of the amplitude is in the fundamental harmonic. In the latter the syrinx operates below a certain threshhold frequency (the level of which depends on various characteristics of the syrinx), below which the oscillations cease to be sinusoidal. As the operating frequency is lowered, there is a gradual shift in dominant amplitude from the first to the second, then to the third and higher harmonics.

The sound produced in either domain "can be modulated, in either frequency, or in amplitude, or more usually in both, with extraordinary rapidity, so rapidly in fact that human ears cannot perceive the modulations as such, receiving instead an impression of notes of varying quality or timbre" (Greenewalt, 1968, p. 176). The two forms of modulation, amplitude (AM) and frequency (FM), may or may not be related to each other and, if they are related, the relationship may be direct or inverse.

A further phenomenon greatly increases the information potential of an individual bird's song. Borror and Reese (1956) and Thorpe (1961) showed that some birds produce simultaneous and acoustically unrelated frequency patterns, suggesting that the right and left halves of the syrinx operate independently. Greenewalt (1968) demonstrated that this situation is widespread among birds of many orders and that the independence of the two sources is nearly complete. They may operate simultaneously or at different times—often one voice is starting as the other is tapering off—in the same or different domains, and with the same or different AM-FM relationships.

Greenewalt (1968) postulated a mechanism of avian sound production based on earlier work by Setterwall (1901), Rüppell (1933) and Miskimen (1951) and on applications of acoustic theory to current knowledge of syringeal structure and of vocal characteristics. It is generally agreed that the internal tympaniform membranes (ITM) are the primary source of sound vibrations and that their vibrating frequency depends on tension controlled by the syringeal muscles. Greenewalt suggested that this tension is produced by a pressure differential between the interclavicular air sac (surrounding the syrinx) and the lumen of the bronchus. Each ITM is an independent vibrator. With the bronchus prevented from collapsing by the C-shaped elements, the ITM bulges inward, constricting the air passage. Greenewalt also suggested that the passage would be constricted through the tension of the syringeal muscles, but it seems to me that the muscles, if they increase membrane tension, would tend to draw the ITM out of the bronchus, reducing the constriction of the passage. Changes in the shape of the B-elements, induced by the muscles, would probably also alter the degree of constriction of the bronchial passage, but it is difficult to predict how this would affect membrane tension and vocal output.

Chamberlain et al. (1968) manipulated muscles in the excised syrinx of the common crow (*Corvus brachyrhynchos*) and concluded that the primary role of the intrinsic muscles is to control the positions of A-1 (their B-3) and B-1 (their B-4), the latter rotating around its long axis to increase tension on the external tympaniform membrane (ETM). The passage is constricted by the physical insertion of the anterior edge of B-1 as it rotates inward. The moving air further constricts the passage, by the Bernoulli effect, and sets the membranes, internal and external, into vibration. Chamberlain et al. noted that the ventral end of A-1 has a ventromedial cartilage (the "cartilago tensor" of some earlier authors) that "turns the i.t.m. close to the e.t.m." The muscles acting on A-1 were found to be M. bronchialis anticus, M. bronchialis posticus, and M. bronchotrachealis posticus.

Vibrations of the internal tympaniform membranes thus provide the basic vocal frequency or "carrier frequency" (Stein, 1968). Greenewalt and Stein have both noted that the external tympaniform membranes are too thick for high frequency vibrations. Stein postulated that frequency modulations might arise from a second oscillator in the ETM and external labium. Greenewalt suggested that modulating oscillations might be present in the syringeal muscles themselves.

It is evident from the studies of Miskimen (1951) and Chamberlain et al. (1968) that control of each tympaniform membrane is vested in several muscles and that a single muscle, through complex movements of the element of insertion and through ligamental connections with other elements, may affect more than one element, labium or membrane. The roles of the various parts of the syrinx in producing the complex sounds described by Greenewalt and his many predecessors will be elucidated only by careful *in vivo* and *in vitro* observations of the syrinx in action.

Usually neglected in discussions of syringeal function is the fact that oscine songs are both learned and innate. Andrew (1957), Hinde (1958), Lanyon (1957), and others have demonstrated that adult song is the result of innate factors, reception of songs of other individuals, rehearsal and feedback. The uniformity of syringeal structure among oscines suggests that inherited and acquired patterns in the central nervous system usually play a far greater role in determining the characteristics of song than do patterns of syringeal musculature. I have examined the syringes of individuals of several pairs of sympatric sibling species that rely largely on song for species recognition. The syringes of the eastern and western meadowlarks (*Sturnella magna* and *S. neglecta*) are indistinguishable, yet their songs are strongly different (Lanyon, 1957). The situations in the European warblers *Sylvia borin* and *S. atricapilla* (cf. Thorpe, 1961) and in certain North American flycatchers of the genus *Empidonax* (cf. Stein, 1958) closely parallel that in meadowlarks.

What relationship, if any, exists between the complexity of the syrinx and that of the song? Greenewalt (1968) asserted that certain non-passerines and non-oscine passerines produce songs as complex "as those characteristic of the most accomplished oscines," considering complexity in terms of elaborate modulations. The better songsters among the oscines, he noted, are capable of greater variety in their songs, and in certain species there is a greater individual frequency range than any found in non-oscines. Greenewalt felt that the complex oscine syrinx offers little or no functional advantage over the simple syrinx found in most non-passerines and in certain passerines.

A review of accounts by field observers provides a somewhat different picture, but we must remember that Greenewalt is comparing specific cases, not general trends. Passerines with the pico-passerine type of syrinx produce rather simple calls, most of which can hardly be termed songs, and there is certainly a trend toward longer and more elaborate songs from the broadbills to the oscines. The broadbills (Eurylaimidae), pittas (Pittidae) and most of the "typical" cotingas (Cotingidae) utter whistled notes or harsh calls, either virtually unmodulated or slowly modulated. Descriptions of the songs or calls of this group vary depending on the listener. The predominant characteristics are the use of short notes repeated rhythmically, or long, steady notes, usually with little change in pitch. Smythies' (1940, p. 289) description of the vocalizations of the broadbill *Psarisomus dalhousiae* is typical of this category: " a not unmusical, rather shrill, loud whistling call of five to eight notes all on the same pitch; a soft churring note when feeding; an occasional single 'weet' call; and several harsh tin-kettley notes when annoyed."

Among the Tyrannidae and Pipridae the spectrum of vocalizations runs from notes as simple as those of the broadbills to songs, as noted above, as complex as those of oscines. In all cases the individual repertoire is limited. The majority of flycatchers and manakins produce relatively simple songs, however, and it is safe to state that, as a group, they are less accomplished than the oscines. A comparison between syringeal and vocal complexity within the Tyrannidae would undoubtedly prove interesting.

In the lyrebirds (*Menura*) and scrub-birds (*Atrichornis*) the use of song is highly developed. The most striking vocal feature of these birds is that most of the vocalizations are imitations of the songs of true songbirds (oscines) and non-passerines. To the human ear the pitch, melody and timbre (overtones) of lyrebird imitations are indistinguishable from the songs on which they are modeled. Individual lyrebirds also learn to imitate mammal calls, mechanical sounds, and even the rustling noise produced by the feathers of cockatoos (Chisholm, 1951). The scrub-birds are second only to the lyrebirds as mimics. I know of no acoustical analysis of lyrebird songs comparable to that done by Thorpe (1959) of mimics of the human voice. Robert C. Stein (personal communication) found the songs of lyrebirds to resemble only superficially the songs on which they are based. Certainly the vocal ability of the Menurae, which have slightly simpler syringes that the oscines, demonstrated the importance of non-syringeal factors in singing "ability."

Taken collectively, the oscines amply deserve the name "songbirds," for they include virtually all of the species commonly associated with elaborate, melodious voices, pleasing to the human ear. Acoustically the group includes an extreme range of vocal abilities. Some, such as the swallows, waxwings, and pipits, are capable of less elaborate or varied songs than are found in many suboscines. In other songbird families, notably the thrushes (Turdidae) and sparrows (Fringillidae), many species are distinguished by elaborate and varied songs and large individual repertoires. Despite the large amount of variation in vocalizations among the various oscine families, the syrinx is of about the same complexity throughout the suborder. In more vocal groups (and sometimes in male individuals) the volume of syringeal musculature is larger than in those groups that sing less and, particularly, that sing less loudly. Evidently the major factor in vocal diversification in the oscines has been changes in the nervous system, rather than in syringeal structure.

REVERSIBILITY AND EVOLUTIONARY TRENDS.

A concept fundamental to the past use of syringeal morphology in passerine taxonomy is that the evolution of the syrinx has proceeded from the simple to the complex in a smooth series. Garrod, Forbes, and most of their contemporaries seem to have accepted as axiomatic the idea that syringeal evolution has moved in one direction only, toward complexity. The evidence is largely circumstantial. There are no known passerines (and very few nonpasserines) that do not use vocalizations in some aspect of their existence. Selection seems to have favored considerable reliance on vocal communication and functional degeneration of the syrinx would be maladaptive. One can conceive of a population in which vocalizations have lost their biological significance in favor of some other form of communication. Selection in such a population might favor simplification of the tracheobronchial junction, perhaps for respiratory advantages. Selection of this type may have been responsible for the absence of any tracheobronchial specializations in the New World vultures (Cathartidae). The lack of a syrinx in the Cathartidae was first noted by MacGillivray (1838) and has been "discovered" by several authors since then (Wunderlich, 1886; Gadow and Selenka, 1893; Beddard, 1898; Maynard, 1928; Miskimen, 1951).

Perhaps the least vocal of passerine birds are certain of the "arena" species, such as the cocks-of-the-rock (*Rupicola*) and some manakins (*Pipra* and *Manacus*), in which vocal sounds are partly replaced by mechanical ones (Snow, 1962). Eugene Eisenmann informs me that outside their arenas even these manakins are quite vocal. Although largely silent in the dancing arenas, cocks-of-the-rock have several notes used for communication among males (Gilliard, 1962). In the large majority of other passerines the reliance on vocal communication is such that even slight functional impairment of the syrinx would seriously penalize its owner in reproduction.

The extent to which tracheal modifications have gone in a few species suggests that the interference by the syrinx with respiration is not great. Extended coiled trachea are found in several non-passerine groups (swans, cranes, and some sandpipers). One might expect the longer trachea to be disadvantageous in breathing, but apparently the vocal advantages outweigh any respiratory disadvantages. The only passerine birds known to have extended tracheae are the Trumpet Birds (Paradiseidae, *Manucodia*) in which the length of the trachea may be as much as five times the length of the bird without its tail. (Forbes, 1882b). Two specimens of *Manucodia* measured by me had body lengths of about 150mm (from beak to pygostyle) and tracheae 522 and 836 mm long. The trachea forms a flat coil between the skin and the pelvic musculature. A long trachea must greatly increase the amount of residual air in the respiratory system, but it apparently allows the bird to produce a sound of exceptional carrying qualities.

In most passerines the respiratory disadvantages are less obvious, but one might expect that in the absence of continued selection for an elaborate syrinx the tracheobronchial region would revert toward the simpler primitive state. In some oscines of limited vocal abilities, such as swallows and waxwings, the syringeal musculature is very thin, but the same muscles are present as in other oscines. The small size of the internal tympaniform membranes in the bronchi of swallows may be due to a requirement of high pressures in the lungs or in the interclavicular air sac, correlated with their highly aerial existence. The swifts, which may be considered nonpasserine counterparts of the swallows, have well-developed internal tympaniform membranes (Beddard, 1898) despite apparent similarities in respiratory requirements.

I know of only one case in which the present syringeal structure suggests that muscles have been lost. The New Zealand Wrens, *Xenicus* and *Acanthisitta,* possess a well-developed drum but no intrinsic muscles. In other passerine groups extensive fusion of elements is correlated with well-developed intrinsic musculature. It is possible that the drum in the Acanthisittidae evolved in conjunction with strong syringeal muscles that have since been lost. Published accounts differ concerning the singing abilities of the New Zealand Wrens. Guthrie-Smith (in Oliver, 1955) mentioned "a loud 'cheep'" as the alarm note of *Xenicus longipes,* whose "conversational notes are a faint rasping sound." M'Lean (1911) felt it doubtful that *Acanthisitta chloris* has a real song and mentioned a faint call note "sit" and a rattling alarm note "str-r-r-r." Potts (in Dawson and Cresswell, 1949) mentioned the "twittering song" of this species. Watters (1950) wrote of its "distinctive 'cheep'." Certainly the Acanthisittidae have a limited vocal repertoire compared with other passerines. Unfortunately so little is known of the anatomy of this family that the significance of their unusual syrinx cannot yet be understood.

If we accept the current idea that the oscines are the most highly evolved of passerine birds, it is quickly evident that the trend has been toward greater reliance upon all types of vocal communication. There is some circularity in this conclusion, for syringeal structure and elaborate songs have been a major factor in the current placement of the oscines. Regardless of the evolutionary order, seems to be a general correlation between the intricacy of the syrinx and the complexity and biological importance of song.

THE FIRST PAIR OF SYRINGEAL MUSCLES.

I have suggested above that the ancestral pico-passerine syrinx lacked intrinsic syringeal muscles. From this condition intrinsic muscles could have evolved either *de novo*, i.e., without a direct relationship to any previously existing muscle, or through the subdivision of one of the extrinsic muscles.

De novo appearance of an intrinsic muscle seems possible, but is difficult to demonstrate. Genetic control over muscle formation has not been studied, but it seems unlikely that a discrete functional muscle would appear through a single mutation. If a mutation should lead to the appearance of a few fibers in a part of the syrinx previously devoid of muscle, and if the new fibers were functionally advantageous, they might provide the basis for the evolution of a new muscle.

The second form of origin of new muscles, through the division of existing ones, appears to be more easily demonstrated. The configuration of extrinsic and intrinsic muscles in some birds may be of aid in identifying the "parent" muscle. This is particularly true in the few cases, discussed below, in which the evolution of the new muscle appears to be incomplete. Of the two extrinsic muscles, M. tracheolateralis seems more likely than M. sternotrachealis to produce an intrinsic muscle. Evolution of an intrinsic muscle from an extrinsic one requires that the latter be in contact with the trachea for part of its length. In most modern birds M. sternotrachealis extends from an origin posterior to the syrinx obliquely to its insertion, with little direct contact with the trachea except in the region of insertion. Derivation of the first intrinsic muscle from this type of M. sternotrachealis would require not only a new subterminal attachment, but also a complex rearrangement of the resultant muscles to attain any known configuration.

The derivation of the first intrinsic muscle from M. tracheolateralis is not only evolutionarily possible, but is sustained by evidence from modern forms. Hypothetically the pattern of this change would be as follows: 1) Primitively, M. tracheolateralis extends down each side of the trachea to insert on a lower A- or B-element. The muscle is loosely attached to the trachea by elastic connective tissue along its entire length. Symmetrical contraction of both Mm. tracheolaterales results in shortening the trachea (unless opposed by the Mm. sternotracheales) and in moving the elements of insertion relative to the adjacent elements. 2) A condition gradually evolves in which the attachment of the muscle to one of the underlying A-elements (A-6, for example) is strengthened. Such an attachment, if accompanied by appropriate innervation, results in more sensitive control over the element at the terminus of the muscle at some sacrifice of distance through which the element may be moved. 3) If favored by selection, the intermediate attachment becomes stronger, resulting in an insertion on A-6 for the anterior portion of the muscle and a new origin for the posterior portion. 4) Ultimately there is complete loss of fiber continuity across the new attachment and the posterior section may be considered a distinct muscle. Although bilateral symmetry is not a requisite of the process described above, it would probably be selectively advantageous, by reducing the distortion of the syrinx during muscle contraction.

The increase in attachment that results in the new muscle might be one of two types: a) Starting with the deep fibers across the full width of M. tracheolateralis, it could involve more and more superficial fibers until the entire thickness of the muscle is attached, or b) starting at one edge with the full thickness of the muscle, it could expand across the muscle until all of the fibers are attached. The end result is the same in the two cases. The new muscle has its dorsal and ventral edges in line with those of the anterior portion (which may still be called M. tracheolateralis); its fiber direction and direction of action are the same as those of the parent muscle; and its insertion is the same as previously.

The present syringeal structure of some members of the Tyranni suggests that both types of derivation from M. tracheolateralis may occur. In the cotinga *Xipholena* and the tyrannids *Myobius* and *Pyrrhomyias* there are no intrinsic muscles, but some deep fibers of M. tracheolateralis are attached to one or two elements of the trachea some distance from the insertion of the muscle. The attachment is weak, involving only connective tissue, without apparent interruption of fiber continuity.

In one specimen of the manakin *Schiffornis turdinus,* the interrelationships of the extrinsic and intrinsic muscles suggest that the latter arose from the former. The well-developed intrinsic muscle is covered by a thin layer of the superficial fibers of M. tracheolateralis. The deeper fibers of the extrinsic muscle insert immediately anterior to the origin of the intrinsic muscle. In *S. virens* and in the other specimen of *S. turdinus,* the intrinsic muscle is nearly identical but is not covered by *M.* tracheolateralis, all of which inserts as do its deeper fibers in the anomatous specimen of *S. turdinus.*

A possible example of the evolution of an intrinsic muscle through the attachment of one edge of M. tracheolateralis is found in the small tyrannid *Tachuris rubrigastra* (Pl. 13). The long, narrow intrinsic muscle, M. obliquus ventralis, is paralleled by a long dorsolateral branch of M. tracheolateralis, while the short ventral fibers of the latter insert immediately anterior to the origin of the intrinsic muscle. This configuration could also have arisen through the complete "cutting off" of the terminal part of M. tracheolateralis, followed by broadening and then elongation of the old muscle into a position adjacent to the new muscle.

Evolutionary shifts in muscle attachments are discussed in a separate section (below).

The use of modern species as examples of intermediate situations should not be inferred to mean that they themselves are ancestral to existing birds with fully evolved intrinsic muscles. The presence of "half-evolved" intrinsic muscles in *Xipholena*, *Myiobius* and *Pyrrhomyias* may mean that these groups are still evolving intrinsic muscles, or merely that this type of musculature is optimal for producing the types of vocalizations favored in these birds.

In addition to birds possessing a single pair of intrinsic muscles, there are many with balanced dorsal and ventral muscles. Examples of the balanced type include all of the woodcreepers (Dendrocolaptidae) and ovenbirds (Furnariidae), one manakin (*Corapipo*), lyrebirds and scrub-birds (Menurae) and oscines (Passeres). The dorsal and ventral muscles originate on the trachea at the insertion of M. tracheolateralis and insert at the respective ends of certain cartilaginous elements. These intrinsic muscles could have evolved consecutively, but in view of their balanced action, it seems more likely that they appeared simultaneously. If so, their evolution probably involved both the formation of a subterminal attachment and the splitting into two fasciculi at the insertion. Either of these changes could have happened first, or they could have occurred at the same time. The insertions of the fasciculi then shifted to the ends of the elements on which they inserted. In view of differences in the cartilages, it is likely that this process occurred separately in at least three lines of evolution, leading, respectively, to the woodcreepers and ovenbirds, to *Corapipo*, and to the Menurae and oscines.

Additional Intrinsic Muscles.

In addition to the dorsoventrally symmetrical muscle systems just discussed, there are syringeal patterns among the Tyrannidae that involve two pairs of intrinsic muscles. The possible sources of the second muscle are similar to those of the first: *de novo*, from M. tracheolateralis, or from the first intrinsic muscle. The arguments concerning *de novo* appearance are the same as for the first muscle, with as little evidence, and need not be repeated.

In the Olive-sided Flycatcher (*Nuttallornis*) the short lateral intrinsic muscle, M. obliquus lateralis, is isolated from the ventral intrinsic one, M. obliquus ventralis, by an extension of M. tracheolateralis (see Pls. 9 and 10). In *Empidonax*, *Myiochanes*, and other flycatchers believed to be closely related to *Nuttallornis*, the lateral intrinsic muscle is absent and its place is occupied by the extrinsic muscle. M. obliquus lateralis in *Nuttallornis* could have resulted from a "cutting off" of the lateral terminal region of M. tracheolateralis in the manner postulated above for the evolution of the first intrinsic muscle. M. obliquus lateralis could also have been derived from M. obliquus ventralis prior to the shift of the latter into its present position. This derivation presumes an earlier divergence of *Nuttallornis* from *Empidonax* and *Myiochanes* than is suggested by other features of their anatomy.

In many tyrannids with two pairs of intrinsic muscles, the evidence suggests that the second evolved from the first. In the genus *Elaenia* and its relatives, the second muscle seems to have evolved only recently. The two intrinsic muscles lie closely adjacent, with their insertions continuous and their origins barely separated (not quite separated in one individual of *E. chiriquensis*). The process of change from one muscle to two seems to have involved a gradual increase of the muscle fibers at the two edges of the broad intrinsic muscle and subsequent or contemporaneous loss at the middle. If the two intrinsic muscles provide better modulation than one, it is reasonable to assume that their appearance in the large genus *Elaenia,* with many similar sympatric species, reflects the use of voice in species isolation.

In *Myiarchus*, another large tyrannid genus containing many sympatric species, vocalizations are the most important means of species recognition (Lanyon, 1963). Apparently some populations, and possibly whole species, are in the process of evolving a second intrinsic muscle through a process like that in *Elaenia*. It is doubtful that complete separation of the lateral head of the muscle has taken place. Miskimen (1963) described a discrete lateral muscle, but the degree of separation found was not stated. It would be interesting to compare large numbers of individuals of sympatric *Myiarchus* species with individuals of species whose ranges do not overlap with other *Myiarchus*.

The pattern of evolution of the short muscles in the lyrebirds and oscines appears to have been different from the evolution of M. obliquus lateralis of the Tyrannidae. M. bronchialis posticus is a short deltoid muscle originating along a line that extends from the lateral surface of the drum at about A-5 in a spiral toward the dorsal surface at A-8. The precise position is variable, but usually most of the origin is lateral. In the Mynah, *Gracula religiosa*, the dorsal limit of the origin is continuous with the origin of the longer dorsal muscle, M. bronchotrachealis posticus. The insertions of the two posticus muscles are usually on the same element, A-2, sometimes also on A-3. It is likely that the shorter muscle evolved through a separation of the deep fibers of M. bronchotrachealis posticus together with a posteroventral shift in the origin of these fibers. In their present form the two muscles are very close in the lyrebirds and in many oscines, with the longer muscle partly covering the shorter one.

A fourth intrinsic muscle, M. bronchialis anticus, is found only in oscines. The logical "parent" of this muscle is M. bronchotrachealis anticus, a long muscle that lies superficial to it. M. bronchialis anticus originates on the ventral and lateral surfaces of the drum at the level of A-7 or A-8 and sends a fasciculus on each side of the long muscle; one, pars medialis, inserting on the ventral end of A-2 or A-3, the other, pars lateralis, on the ventral end of A-1. Usually the fasciculi of M. bronchialis anticus are in contact beneath M. bronchotrachealis anticus, but in some families the fasciculi insert separately. The evolution of the short muscle probably involved the same mechanism as suggested above for M. bronchialis posticus.

CHANGES IN MUSCLE SHAPE AND ATTACHMENT.

Changes in the shapes of muscles and shifts in their attachments are important factors in the evolution of syringeal complexity. The "ease" with which modifications can be evolved in a population probably depends on their effect on syringeal operation, the extent of genetic change needed to produce them, and the importance to the individual of vocal conformity.

The oblique ventral muscle found in most tyrannid flycatchers appears to have evolved from one in which the fibers were anteroposteriorly oriented. In many tyrannids M. obliquus ventralis is a short, broad muscle in which only the ventral fibers are oblique (see, for instance, *Lichenops*, Pl. 7). The oblique ventral fibers apparently confer a vocal advantage over straight ones in certain situations, for frequently the whole muscle is oblique (*Empidonax*, *Pogonotriccus*, and *Leptopogon* are examples). This condition probably evolved through the gradual increase ventrally of the oblique fibers with the loss of the lateral ones. Sometimes, as in *Empidonax*, the insertion of M. tracheolateralis appears to have moved posteriad into the space beneath the intrinsic muscle. Changes in the type of origin have often followed the shift of M. obliquus ventralis. When its origin is directly on the tracheal elements, the deep fibers must be shorter than the superficial ones. In a short thick muscle, such as that in *Tyrannus,* the deep fibers are only about one-third as long as the superficial ones, a condition that must reduce the mechanical efficiency of the muscle. Greater uniformity of the applied force results if all of the fibers are the same length and this has been approached in some genera (*Empidonax*, *Elaenia* and others) by the evolution of a midventral tendinous raphe at right angles to the fibers. If the Mm. obliqui ventrales operate simultaneously and are attached to opposite sides of the raphe, the latter has little mechanical function other than to anchor the muscles to the trachea when at rest. In the specimen of *Aphanotriccus* examined the raphe extends only about nine-tenths the width of the muscle. In *Arundinicola* only about two-thirds of the fibers are attached to the raphe, the remainder being continuous between the pair of muscles. In some populations and possibly entire species of *Sayornis* the raphe is wholly lacking, all the superficial fibers being continuous across the midline. The conditions found in *Aphanotriccus* and *Arundinicola* suggest that the raphe was once present in *Sayornis.*

Tendinous insertions are evidently acquired rather easily in some genera. The syrinx is rather uniform in *Elaenia,* but in some species M. obliquus ventralis inserts by a tendon to B-1, in others directly on A-1. In both cases the fibers terminate at A-1, suggesting that the tendon was derived from the A-1/B-1 membrane rather than from the connective tissue of the muscle itself. It would seem a simple step to convert the superficial layer of the tough A-1/B-1 membrane into a broad thin tendon, leaving the deeper layers intact.

Evolution of Cartilaginous Elements.

Evolutionary modifications in syringeal musculature are almost invariably accompanied by changes in the related cartilages. The changes may be limited to the existing cartilages or they may involve the acquisition of new elements. Modifications of the existing cartilages may involve width, thickness, radius of curvature, shape, consistency, and fusion. Most alterations appear to occur as responses to changes in stress, either within the syrinx or from other sources.

In every passerine whose syrinx has been studied, there are some muscles for vocalization in the tracheobronchial region and the cartilages in this region differ from those elsewhere in the trachea and bronchi. The major modification of the cartilaginous elements in the simplest syrinx is a broadening and thickening of the elements on which muscles insert. The acquisition of broader and thicker muscles is usually associated with expansion and sometimes fusion of those elements whose movement would be detrimental to vocal control. If the syrinx is composed of narrow elements with wide spaces between them, contraction of a muscle parallel to the tracheal axis results in shortening the syrinx along the entire length of the muscle, instead of moving only the element on which it inserts. Either action could be selectively advantageous. Where the muscle axis is entirely parallel to the axis of the syrinx, the force may be restricted to the element of insertion by the elimination of the membranous spaces between elements. In the flycatcher *Pitangus sulphuratus* the lower A-elements are closely fitted together but not fused. In most other cases in which the elements are in close contact with one another there is fusion at a few points.

When the direction of muscle force is not parallel to the syringeal axis, the cartilaginous elements are subjected to shearing and torsion stresses, in addition to compression. The problem is alleviated by the fusion of two or more elements into a drum. The fusion may be incomplete, as in the tyrannids *Pogonotriccus* and *Tolmomyias,* or complete, as in many other tyrannids, some manakins, woodcreepers and ovenbirds, and most, if not all, oscines.

Accessory syringeal cartilages are of two types in the passerines: the Processi vocales of the Furnarioidea and the internal cartilages found in many of the Tyrannoidea. In both cases the evolution of the accessory cartilages has advanced so far that their derivations are obscure.

Processi vocales are found in all members of the Furnarioidea. They vary in form from thin curved plates to thick rather narrow rods. Their position is always lateral and they are usually anchored to the large, non-attenuate lower elements. The Processi might have evolved through one of several means: 1) *de novo,* formation in the membrane surrounding the lower trachea; 2) anteriad extension of one of the lower A-elements; 3) coalescence of the lateral regions of the elements now adjacent to the Processi; 4) formation in the tendon of a syringeal muscle, probably M. tracheolateralis, in a manner similar to the formation of sesamoid bones.

De novo formation may form the basis for the present Processi, but there is little information bearing on this form of origin. The manner in which the internal cartilages blend into the surrounding membranes suggests that the change from thick membranes to thin sheets of cartilage is not a severe one. The Processi vocales could have evolved through the formation of a thin sheet of cartilage in the membrane surrounding the lower trachea.

If the Processi had evolved from anteriad extensions of some lower A-elements, one would not expect to find fusion seams, which are frequently present, where the processi are rigidly attached to the elements. The woodcreeper *Drymornis* is the only example in this study in which the Processi are integral parts of the lower A-elements. *Drymornis* is unique in having both of the elements carrying the Processi divided, resulting in exceptional flexibility in that part of the syrinx.

Coalescence of the lateral regions of several A-elements seems unlikely to have led to the Processi for in many modern species (most Formicariidae and Rhinocryptidae) careful removal of the Processi reveals intact elements underlying them.

The fourth alternative, formation in a tendon, is a very likely means of evolution of the Processi. In many Formicariidae (*Taraba,* for instance) the Processi are little more than tendinous straps with cartilaginous centers. The edges of the Processi are firmly bound to the surrounding connective tissue, a situation very similar to that of the sesamoid bones of many tendons. This evolutionary pattern supposes that the Mm. tracheolaterales originally inserted on one of the lower A-elements by a tendon or that such a tendon evolved concurrently with the Membranae tracheales. The evolution of a rigid plate in the tendon would provide more direct control over the lower elements, compensating for the flexibility caused by the presence of the Membranae. Of the alternatives suggested above, the "sesamoid" hypothesis seems to me the best supported by the morphology of recent furnarioids.

The internal cartilages lie in the anterior dorsal part of the internal tympaniform membranes in most tyrant flycatchers, a few cotingas (*Attila* and relatives), a New Zealand Wren (*Acanthisitta*) and an asity (*Neodrepanis*). Small ventral cartilages sometimes lie in line with the ventral ends of one of the B-elements, suggesting that they might be remnants of an element that was once double. The position of the internal cartilages relative to the other elements must depend strongly on their acoustic function. The large dorsal internal cartilages have no clear alignment with any elements, although frequently attached to one or more of them. In some tyrannids (*Capsiempis, Leptopogon*) the internal cartilages are very thin at their edges and blend so gradually into the membranes that only histological examination would show where one begins and the other ends. In short the internal cartilages are nearly always more strongly associated with the internal tympaniform membranes than with the supporting elements of the syrinx, with which they sometimes have no connection. It seems likely that the internal cartilages evolved in the membranes, but the exact pattern of their evolution is likely to remain unknown.

Another syringeal component subject to evolutionary change is the pessulus. This midsagittal bar is found in all passerines except the Furnarioidea, most of the Pittidae, many of the Tyrannidae, and the oscine family Alaudidae (larks). When present, the pessulus does not appear to have undergone much elaboration, except in a few isolated cases. The selective pressures affecting the pessulus are difficult to evaluate, for its role in vocalization is unknown. Situated at the junction of the internal tympaniform membranes, it must be instrumental in functional isolation of the right and left halves of the syrinx, preventing tension on one side from affecting the other. Lying in the dorsoventral diameter of the lower end of the syrinx, the pessulus also prevents compression of the drum or other lower elements.

The evolutionary loss of the pessulus in the Furnarioidea may well be correlated with the need for dorsoventral flexibility. Certainly the Membranae tracheales, with the attenuated elements crossing them, result in exceptional flexibility of the syrinx. In no known furnarioid are there modifications for rigidity in this region as are found in some other types of syringes, in which elements are fused. There are occasionally only divided elements posterior to the Membranae. Selection in this group appears to have favored flexibility in the region of bifurcation and the loss of the pessulus is one means of obtaining such flexibility.

In most tyrant flycatchers in which the pessulus has been lost, its position has been nearly occupied by the medial sections of double A-elements e.g., (*Tyrannus, Myiarchus, Inezia*), or by a broad "plug" of soft cartilage (*Sirystes, Xolmis*). The "plug" cannot be considered a derivative of the pessulus for frequently both are present. Some species of flycatchers appear to be evolutionarily losing the pessulus, there being individuals with, those without, and intermediates. In the intermediate situation the pessulus is a short rod extending only partway from one surface of the syrinx to the other. That this condition exists in a number of morphologically dissimilar syringes belong to tyrannids not usually considered closely related (*Leptotriccus*, *Blacicus*, *Legatus*) suggests that the pessulus is being reduced independently in several evolutionary lines. It will be interesting to determine the complete pattern of distribution of the pessulus among individuals and species of *Tyrannus* and others of the family.

In the pittas lacking the pessulus no elements have assumed the position of the pessulus and the internal tympaniform membranes are continuous from one side to the other, meeting in a smooth curve. The simple syringeal musculature, with its force directed parallel to the tracheal axis and its insertion on the lowest of several divided A-elements probably does not exert a dorsoventral stress in the region of bifurcation. The voices of many pittas have been described. *Pitta arcuata* has "a melancholy whistle" (Shelford, *in* Smythies, 1960) and *P. granatina* a whistled "mellow and musical strain" (Adams, *in* Smythies, 1960). According to Smythies (1940) *P. nipalensis* "is said to have a magnificent double whistle" (i.e., two successive notes). From many similar accounts it is evident that the pittas rely on simple songs, frequently of considerable volume. Careful electronic analysis is needed to determine the role of the membranous continuity in their syrinx.

The absence of the pessulus in the larks does not appear to be correlated with reduced singing "ability" for the family has long been famous for their vocal displays. The striking features of the display are the volume and duration of the song and the flight accompanying it. Tucker (in Witherby et al., 1938, p. 181) described the song of the Skylark, *Alauda arvensis*, usually considered the most musical of the Alaudidae, as being "delivered with great spirit and vehemence . . . a loud, clear, shrill warbling, pleasingly modulated, though of limited compass, sustained unbroken up to 3 or occasionally as much as 5 or more, minutes." Larks occupy large territories in open areas and the males sing while rising to a height of several hundred feet above ground.

Phylogeny, Homology and Taxonomic Characters.

As pointed out by Mayr et al. (1953 p. 42), "it is the avowed aim of a modern classification to reflect phylogeny." The evolutionary taxonomist must erect, either in his mind or on paper, a tentative phylogeny for the group under consideration, remaining aware that his phylogeny is an attempt to organize events that really happened. Consideration of passerine phylogeny is made more difficult by the virtual lack of pertinent fossil material and by repeated instances of convergence and parallelism.

In erecting a phylogeny based on a single system of interdependent characters, such as the syrinx, one must admit that some lines of evolution have several alternatives and that others do not lend themselves to phylogenetic interpretation at all. There are several possible evolutionary lines, discussed below, that could have led to the syringeal patterns of the modern lyrebirds and scrub-birds. The determination of which line was the actual one has important bearing on the use of the syrinx in the taxonomy. The syringeal structure of the Eurylaimidae, Pittidae, and Cotingidae is of little use in determining the phylogeny of these groups. On the other hand, within the superfamily Furnarioidea syringeal morphology indicates a definite phylogeny more likely to have occurred than other alternatives. I have avoided presentation of the usual phylogentic "tree," because such a diagram cannot be adequately drawn from the syringeal evidence. I will discuss the phylogeny of the various passerine suborders from the aspect of syringeal morphology, drawing occasionally on other anatomical data to clarify certain lines of evolution.

EURYLAIMI.

The simple syringeal pattern of the broadbills is not of great phylogenetic significance, beyond indicating that they have not advanced vocally over the pico-passerine ancestor.

FURNARIOIDEA.

This superfamily of the suborder Tyranni has the most clearcut phylogeny, from the syringeal point of view, of any passerine group, but their syrinx suggests nothing about their relation to other groups. The Membranae tracheales were probably nearly or wholly evolved before the group diversified into the wide variety of forms present today. The Membranae are the most uniform feature of the furnarioid syrinx, except for the absence of the pessulus. Apparently the pessulus was lost early in the evolution of this group, for no trace of it has been found in any modern furnarioid. The diversification of syringeal types led to two major stocks. The ovenbird-woodhewer line (Furnariidae and Dendrocolaptidae) evolved a dorsoventrally symmetrical syrinx with two pairs of muscles. The woodhewers evolved more elaborate Processi with projecting horns for the attachment of muscles. It is not clear whether the presence of horns on the Processi in *Geositta* represents an independent appearance from those in the woodhewers.

The other line, which produced the antbirds (Formicariidae) and tapaculos (Rhinocryptidae), contains three basic syringeal types. The simplest of these, found in *Teledromas*, *Formicarius*, *Chamaeza*, *Grallaria*, and *Conopophaga*, is characterized by large Processi and the absence of intrinsic muscles. There is no evidence to suggest that the simplicity found in this group is secondary. Another group is the "typical" antbirds (*Taraba* and similar forms) with small Processi and ventrally originating intrinsic muscles. The third group, the tapaculos (except *Teledromas*), have large Processi with narrow stems and dorsally originating intrinsic muscles. If, as suggested above, the ancestral Processi were of the small "tendinous" type found in most modern antbirds, the evolution of *Formicarius* and similar forms has been away from the typical antbirds and toward the tapaculos. The latter are less advanced than the antbirds in the complexity of syringeal musculature, but seem to have more highly specialized Processi. *Teledromas*, although it has a syrinx nearly identical to that of *Formicarius*, is less divergent from the other tapaculos than *Formicarius* is from the other antbirds.

TYRANNOIDEA.

The New World families included in the superfamily Tyrannoidea include many genera in which the syrinx has advanced little from the hypothetical pico-passerine model. The presence of simple syringes in many cotingas and in some manakins and tyrant flycatchers suggests that the most recent common ancestor of this varied assemblage lacked intrinsic syringeal muscles and cartilaginous elaborations. It is possible that intrinsic muscles evolved in several different lines within the Tyrannoidea and may be still evolving. The presence of internal cartilages in the absence of intrinsic muscles (in *Terenotriccus* and a few other suboscines) suggests that internal cartilages were acquired independently of intrinsic muscles. The latter could have been evolved and then lost in the line or lines leading to *Terenotriccus* and similar forms, but unless the loss occurred prior to the presumed radiation into *Terenotriccus, Pyrrhomyias, Myiobius* and possibly *Piprites*, one would not except to find such homogeneity in the resulting syringes. It is also possible that *Terenotriccus* and the similar birds diverged from the other tyrannids before the appearance of internal cartilages, and that internal cartilages appeared separately in the two stocks.

It is difficult, if not impossible, to determine how many times intrinsic muscles have evolved in the Tyrannoidea. In some genera, such as *Schiffornis,* the evolution of intrinsic muscles appears to be not yet complete. In others intrinsic muscles are fully evolved, but related genera with structurally similar syringes lack them completely. A pair of genera exhibiting this relationship are the manakins *Pipra* and *Manacus.* In a few flycatchers (*Todirostrum, Spizitornis, Mecocerculus*) the alignment of the intrinsic muscle with the extrinsic M. tracheolateralis suggests a recent evolution of the former.

Although intrinsic muscles may have evolved repeatedly in the Tyrannoidea it seems less likely that repeated conversion to oblique ventral muscles has taken place. A truly oblique M. obliquus ventralis is found only in association with internal cartilages, except in the manakin *Ilicura.* We do not know what functional relationship exists between these two features of the syrinx, nor what selective pressures are exerted by the general body plan of the bird. There is a great deal of variation in the degree of obliquity of the intrinsic muscles, but in a large majority of recognized tyrannids as well as the Sharpbill (*Oxyruncus*) and the "cotingas" *Attila* and *Pachyramphus,* many of the ventral fibers are oblique. Considering the heterogeneity of external anatomy in the Tyrannidae, one might well expect to find a greater variety of syringeal muscles than are present, if the oblique quality of the intrinsic muscle had appeared in many separate stocks.

If the oblique intrinsic muscles were present early in tyrannoid evolution, it is reasonable to suggest that *Attila* and the other members of the *Myiarchus* group and *Oxyruncus* (as well as *Iodopleura* and *Ilicura*?) diverged from the tyrannid line later than the more colorful cotingas (*Cotinga, Pyroderus,* etc.) and the *Terenotriccus* group.

The flycatcher species *Machetornis rixosa* provides a particularly difficult phylogenetic problem. The Mm. sternotracheales strongly resemble those of *Xolmis* and other "ground tyrant" flycatchers, yet *Machetornis* lacks intrinsic muscles. The relationship of the size of M. sternotrachealis to the degree of activity during singing is unknown, but this muscle, connecting the syrinx to the sternum, is more likely than the intrinsic ones to be affected by the activity of the individual. External features support the relationship between *Machetornis* and the ground tyrants. If the relationship is real, *Machetornis* must have lost the intrinsic muscles which are found in the others. Perhaps the loss of the intrinsic muscles is correlated with the evolution of long, straight, non-tapered bronchi in *Machetornis.* As might be expected, the song of

Machetornis is simpler than those of the ground tyrants (Hudson, 1920; Wetmore, 1926).

Solutions to many questions of the phylogeny of the syrinx in the Tyrannoidea will appear only when *in vitro* (and, perhaps, *in vivo*) experimentation has analysed the functional significance of syringeal components. Careful comparisons between vocal performance and syringeal structure are needed to supplement *in vitro* studies.

MENURAE.

The two families of this suborder, the lyrebirds (Menuridae) and scrub-birds (Atrichornithidae) are similar to each other in basic syringeal structure. The two pairs of long muscles are similar to those of the oscines, providing much of the basis for the widely-held theory that the lyrebirds and scrub-birds represent early offshoots of the oscine line. There are several possible phylogenetic patterns.

1) The evolution of the oscine syrinx produced first the long dorsal and ventral muscle pairs, then a short dorsal pair and, fourthly, the short ventral muscles. The common ancestor of *Atrichornis* and *Menura* diverged from the ancestral stock after the third muscle pair had been evolved. By this hypothesis the Menurae would be monophyletic, in the narrowest sense of the word.

2) A second hypothesis states that the common ancestor of *Menura* and *Atrichornis* diverged from the oscine line at a time when the syrinx had less than three pairs of muscles and a third pair of muscles evolved in the scrub-bird-lyrebird line.

3) and 4) Either of the above alternatives could be applied separately to *Menura* and *Atrichornis;* the common ancestor is not a necessary part of the hypotheses and must be considered separately. In their cartilages, both genera are intermediate between the pico-passerine syrinx and the oscine one, there being specialization of the lower A-elements in the direction of "intermediary bars," but no fusion to form a drum.

5) A fifth possible alternative, one which I consider rather unlikely, is that *Menura* and *Atrichornis* had an ancestor or ancestors in the oscines and that their more simple syringes resulted from the loss of a pair of muscles and of fusion. The loss of muscles does not seem probable in birds that rely so strongly on vocalization.

PASSERES ("OSCINES").

The great homogeneity of syringeal structure among nearly 4000 oscine species (for about a quarter of which the syrinx has been examined) strongly suggests a single origin for the group. The only significant deviations from the general pattern are the lack of the pessulus in the larks and the presence of double B-elements in the swallows (*Hirundinidae*). Even in these groups the muscle pattern is the same as in the rest of the suborder. It is probable that the present syringeal structure was fully evolved prior to the radiation of the oscines into their present diversity. The success of this syringeal pattern is evidenced by its retention in widely differing oscine families.

Homology.

Past applications of syringeal morphology to passerine taxonomy have been based on the assumption, supported by the investigations of Müller (1847) and Garrod

(1873, 1876), that the syrinx is a conservative structure, i.e., that it has changed slowly during the radiation of the ancestral passerine stock (or stocks) into the diverse body plans now found. One purpose of this study is to evaluate the degree of conservatism in the syrinx, in order to determine which aspects of syringeal structure have taxonomic usefulness.

The degree of diversity in the syrinx is clearly not directly correlated with the external diversity of passerines generally. Members of the suborder Passeres are so uniform in syringeal structure that a noticeable departure from the norm has usually been considered strong evidence of phylogenetic separation. The very homogeneity of the syrinx among the oscines, while enhancing its value as a character for subordinal definition, reduces its applicability at the lower taxonomic levels. Several groups of genera, at roughly the family level, exhibit minor but apparently consistent myological variations that appear useful in establishing relationships. Detailed description of these variations is beyond the scope of this work and more specimens must be examined before taxonomic conclusions may be drawn.

In the suborder Tyranni the rate of change in the syrinx, in relation to changes in the whole bird, has evidently been more rapid than in the Passeres. This conclusion is based on the relative diversity of modern forms. The diversity of the syrinx makes it more useful at the lower taxonomic levels than at corresponding levels in the oscines, wherever consistent similarities and differences among structural groups can be recognized.

Consideration of any feature in a phylogenetically based taxonomy hinges on whether or not the feature is homologous in all members of the group under consideration (Mayr et al., 1953; Simpson, 1961). The term "homology" is employed here in the sense used by Simpson (1961, p. 78) meaning "resemblance due to common ancestry," which I interpret to mean that the feature in question was present in the common ancestor. Bock (1963, p. 283) defined homology in terms of descent from "the same feature in a group possessing a high degree of evolutionary homodynamy." The latter term is "the ability with which the same feature may originate and evolve several independent times within a group of organisms." Bock pointed out that the acceptance of this definition leads to the use of broadly based taxonomic groups, as suggested by Simpson (1961, p. 124). I agree with Reed (1960) that the use of Simpson's broad definition of monophyly leads to a classification that is both vertical and horizontal. Such a classification obscures the attempt to describe real phylogenetic events. In the case of passerine birds, it is unlikely that the fossil record will ever assist us in deciding phylogenetic questions, but I cannot agree with Bock that "pseudohomologous" (basically "parallel") features can never be uncovered without either intermediate or ancestral forms. He has pointed out that such features have their basis in the "genetical-developmental potential", and perhaps this potential, if we could evaluate it, would be useful in determining the phylogeny. Understanding the adaptive significance of a structure aids in the analysis. Examples of known "pseudohomology" cited by Bock were uncovered without the aid of fossil forms and frequently (as in the case of the Madagascar "nuthatch" *Hypositta*) without any intermediate forms. The finch-billed lark (*Rhamphocorys*) would certainly be considered phylogenetically allied to the buntings, were it not for the several alaudine features (including the syrinx) that make it clearly a lark. The probability of uncovering non-homologous features increases as a particular adaptive complex is studied in greater detail and in a greater variety of animals, and as a larger number of adaptive complexes is available for comparison. This should allow one to determine the homology or non-homology of a feature in the narrower sense. If one wishes to employ the narrower concept of monophyly, one must use a narrow definition of homology.

Applied to syringeal morphology, the above considerations underline the handicap imposed by our lack of knowledge of syringeal mechanics. The strictly morphological approach bears fruit, however, when several features of the syrinx can be compared in considerable detail. I am not prepared to state, at this point in our knowledge, that intrinsic syringeal muscles have arisen only once in the Tyrannoidea, nor that conversion to oblique muscles occurred only once. It is possible that the underlying cartilaginous structure of the primitive tyrannoid syrinx was such as to limit the possible muscle configurations. In that event, the repeated evolution of a particular pattern of musculature might be expected wherever selection favored the appropriate vocal pattern. Until more is known about the degree of functional interdependence of the various parts of the syrinx, we can only rely on morphological analyses in drawing inferences about homology.

At lower taxonomic levels, homology of muscle shape or of cartilaginous element configurations is frequently supported by the detailed duplication of a character in several genera. It is at the intergeneric level that homologies are the easiest to demonstrate, through the multiplicity of character details within the syrinx.

The application of syringeal morphology in the Tyrannoidea increases in reliability toward the generic level. At the higher levels relationships are suggested by syringeal similarity, but not as much weight should be attached to the general similarities as may be attached to the more detailed similarities that frequently exist among groups of genera.

For example, nine genera of flycatchers that I term the "*Tyrannus* group" have in common seven myological and cartilaginous features, several of which seem to be so minor as to have only slight functional significance. It is hard to imagine how similarity in such detail could have arisen independently in two lines, starting with a more generalized syrinx. The nine genera of the *Tyrannus* group have external similarities that have caused "skin taxonomists" to consider them closely allied, but even if the nine were externally diverse, homology of the syrinx would remain a strong probability.

A second case, less strongly supported by external morphology, concerns the flycatcher genus *Myiarchus* and several "cotingas" of which *Attila* is an example. The structural agreement is as close as among the *Tyrannus* group, but there are fewer details of similarity. The case for syringeal homology in the *Myiarchus-Attila* relationship rests on muscle shape, element configuration and the shape and number of internal cartilages. The only external character which argues against the *Myiarchus-Attila* syringeal homology is the scutellation of the tarsus, a character now known to be highly plastic.

Taxonomic Applications.

In short, no single feature of the syrinx is taxonomically useful throughout the Passeriformes and different structural characters are valid at the various taxonomic levels. The major characters enumerated below are functionally interrelated to varying and usually unknown degrees. Their ultimate evaluation must lie in the comparison with the non-syringeal characters, together with which they form the basis for the prevailing classification of the order.

1) Gross anatomical features (major modifications involving most of the tracheobronchial region) are limited to the presence of the Membranae tracheales and Processi vocales in the Furnarioidea. In the remainder of the order the differences are more localized and less profound.

2) The absence of the pessulus is a definitive character for the superfamily Furnarioidea and for the oscine family Alaudidae, but in the Tyrannoidea its configuration is highly variable, even within certain species. Further study may prove it to be of use in some subgroups of the tyrant flycatchers, but at best its taxonomic value will be limited.

3) The degree of fusion of syringeal elements must be applied cautiously as a taxonomic character, for it is evidently related to the type and size of the intrinsic muscles. Fusion and muscle patterns are general indicators of the role of voice in the overall biology of a group and probably are related to some external features. In certain cases, such as in the manakin genera *Manacus* and *Pipra*, peculiarities of fusion are probably indicative of phylogenetic relationships.

4) The internal cartilages of the Tyrannidae and a few others appear to be reliable indicators of relationships at the intergeneric level. Their applicability rests on the wide variety found in the flycatchers, their intrageneric uniformity, and their lack of an obvious functional relationship to other syringeal features. While the internal cartilages may be functionally related to other cartilages and to the muscles, the relationship does not appear to restrict the shape of the internal cartilages, which perhaps exert an independent effect on the voice. The internal cartilages have greater taxonomic validity where they have complex shapes, for the morphological groups are more homogeneous and more clearly separable from each other. Knowledge of the acoustic function of these cartilages will greatly aid in evaluating them as a taxonomic character.

5) Minor peculiarities of the cartilaginous elements are among the most useful characters, because they are probably not greatly dependent upon other characters. Such peculiarities include sharp corners on some A-elements (*Tyrannus*), the dorsally extended pessulus (*Colopteryx*), and even extra elements (*Onychorhynchus, Pitta*). Taxonomic application of any of these peculiarities requires the examination of enough individuals to insure that the "character" is not merely an individual variant.

6) The number of intrinsic muscles has classically been a major character in defining the suborders Menurae and Passeres (Müller, 1847; Garrod, 1876; nearly all subsequent authors) and here it appears to be valid. In the Furnarioidea, the number of intrinsic muscles is useful at the family level. The Eurylaimidae and some families of the Tyrannoidea may be defined as lacking intrinsic muscles, but in the manakins and tyrant flycatchers the character is applicable only at low levels. Two genera of tyrant flycatchers that appear from other syringeal and non-syringeal characters to be closely related may differ in the number of intrinsic muscles (viz. *Elaenia* and *Tyrannulus*). The number of muscles is closely related to the overall shape of the total complex of syringeal muscles. The shape and attachments of each muscle must be examined individually and in respect to other muscles before taxonomic conclusions can be based on the number of muscles.

7) Myological details such as the types and positions of muscle origins and insertions and the shapes of muscles are of rather varied applicability throughout the order. The suborder Passeres may be defined as "acromyodean" (Garrod, 1876) in a general sense, but the opposite term, "mesomyodean," is inappropriate for the rest of the order, in which all intermediates from terminal to middle attachments are found. Specializations of shape or attachment, such as the short, thick intrinsic muscles of *Tyrannus* and some similar species, or the ventral layering of the muscles in *Colopteryx*, seem most likely to show phylogenetic relationships. Certain other myological features, such as the origin of M. obliquus ventralis on a median raphe, are consistent among several tyrannine groups, but are too widespread for use in delimiting a group without overriding other syringeal features.

The results of this study confirm the belief of Müller and many subsequent authors that the syrinx is of value in subdividing the Passeriformes. An exception is its application to the definition of the suborder Tyranni. The superfamily Furnarioidea is based on the uniform distribution of several syringeal features, but the Tyrannoidea cannot be defined on the basis of the syrinx. Certain syringeal characters in both muscles and cartilages appear to be useful at about the family and subfamily levels in the New World Tyrannoidea.

SYSTEMATIC CONCLUSIONS

Taken in conjunction with other anatomical characters, syringeal morphology suggests that the Passeriformes be divided into five suborders: Eurylaimi, Furnarii, Tyranni, Menurae, and Passeres (Oscines).

EURYLAIMI.

Eurylaimidae. The broadbills have traditionally been separated from all other passerines on the basis of their plantar vinculum, first noted by Sundevall 1872 and emphasized by Garrod (1877a), and non-bifurcate spina sternalis. Although the simple syringeal structure supports the belief that the Eurylaimidae are primitive, relative to other passerines, it is of little help in understanding their relationships. They have evolved bright plumage in place of the extensive use of vocalizations for species recognition and courtship. In general their calls are monotonic and simple, produced by a syrinx lacking intrinsic muscles and cartilaginous specialization. The green broadbills (*Calyptomena*) possess elaborations of the anterior edge of the internal tympaniform membrane, and of the Mm. sternotracheales, that set them apart from the rest of the family. These differences support their separation as the subfamily Calyptomeninae.

Philepittidae. The syringeal structure of both *Philepitta* and *Neodrepanis* is remarkably like that of the broadbills *Smithornis* and *Psarisomus* (see Pls. 2 and 17), even to minute details of the cartilaginous elements, but the whole organ is relatively unspecialized. Although the plantar vinculum is absent in *Philepitta*, the spina sternalis is non-bifurcate and pterylosis is similar to that of the Eurylaimidae (Forbes, 1881). Whatever their affinities, the Philepittidae appear to have retained a primitive syrinx while most other passerines have evolved some modifications for song.

FURNARII.

The families grouped by most modern systematists in the superfamily Furnarioidea share an elaborate syringeal form not found elsewhere. No structures even remotely resembling the Membrana trachealis and Processus vocalis are found in other passerines. Aside from zoogeographic considerations, there are no characters to ally them particularly to the Tyranni. Pycraft (in Ridgway, 1907) believed that the distinctions of the syrinx were sufficient to justify subordinal status for the Furnarii and I am inclined to agree with him, when other characters are considered. On the basis of syringeal structure and other characters (pterylosis, cranial and sternal osteology) the following four families can be recognized.

Dendrocolaptidae. The syrinx of the woodcreepers is distinguished from those of other members of this suborder in possessing prominent dorsal and ventral horns on the Processi vocales. Only this family and the Furnariidae possess two pairs of intrinsic syringeal muscles. The presence of horns on the Processi of *Geositta* could be taken to indicate that *Geositta* is more closely allied to the woodcreepers than to the ovenbirds (Furnariidae), but it appears to be a fairly typical ovenbird in other respects. It is possible that the need for greater mechanical advantage for the syringeal muscles has caused the evolution of horns in the syrinx of *Geositta*, independently of the Dendrocolaptidae, but in this case one would expect to find horns on the Processi of other ovenbirds, which must have been subjected to similar selective pressures.

Furnariidae. The close relationship of this group to the woodcreepers is indicated by the similarity of syringeal musculature, which sets the two families apart from the antbirds (Formicariidae) and tapaculos (Rhinocryptidae). The ovenbirds appear to be separable from the woodcreepers on the basis of the absence of horns on the Processi vocales (except in *Geositta*) and by the possession of schizorhinal nares (Garrod, 1877a).

Formicariidae. The antbirds may be divided into two groups on the basis of syringeal morphology. The majority of the genera examined, to which I apply the term "typical antbirds," are distinguished by having one pair of intrinsic syringeal muscles, a very small Processus, and M. sternotrachealis bifurcate near its insertion. Examples of this group are *Taraba*, *Dysithamnus*, *Thamnophilus*, and *Myrmotherula*. The second group, the "ground antbirds," is characterized by the absence of intrinsic syringeal muscles, a large Processus, and a simple M. sternotrachealis. To this group belong *Grallaria*, *Chamaeza*, *Formicarius*, and *Conopophaga*. Long-legged terrestrial birds, they appear to be intermediate between the Formicariidae and the Rhinocryptidae. Such intermediacy is suggested by the presence of a four-notch metasternum, classically a rhinocryptid character, in some species of *Grallaria* and in *Pittasoma* (Heimerdinger and Ames, 1967).

Rhinocryptidae. The tapaculos are usually considered separable from the antbirds by the possession of two pairs of sternal notches, but Heimerdinger and Ames (1967) have shown that this character also occurs in the antbirds *Grallaria* and *Pittasoma*. In their syrinx the rhinocryptids possess a simple M. sternotrachealis and a dorsally originating intrinsic muscle. One genus, *Teledromas*, lacks the intrinsic muscle, its syrinx being much like those of *Formicarius* and *Grallaria*. The tapaculos are outwardly similar to the short-tailed, long-legged, ground-living antbirds which they resemble in syringeal structure, but from which they differ in pterylosis (Ames et al., 1968). Only an extensive study of the anatomy, behavior, and other characters of these two groups will determine whether the present family boundaries are natural or artificial.

TYRANNI.

This suborder should probably be restricted to the five New World families of Wetmore's (1960) superfamily Tyrannoidea: Cotingidae, Phytotomidae, Pipridae, Tyrannidae, and Oxyruncidae. The Pittidae can only be judged "incertae sedis" on the basis of our present knowledge. Their simple syringeal structure reflects their use of bright colors rather than vocalizations in species recognition. This syringeal pattern, characterized by the absence of intrinsic musculature and of cartilaginous modifications, does little to suggest the affinities of the pittas. The absence of the pessulus in most pittas probably represents a specialization and cannot be taken as a definite indication of relationship to other forms that lack the pessulus. The pessulus, probably present in the ancestral "proto-passerine" stock, has been lost by several other groups in the order (all the Furnarii, some individuals and species of Tyrannidae, and all of the oscine family Alaudidae), apparently independently. The Pittidae share with the Acanthisittidae the character of bilaminate planta tarsi, but the tendency toward fusion of tarsal scutes is characteristic of long-legged terrestrial birds. The New Zealand "wrens," consisting of the genera *Xenicus* and *Acanthisitta,* were placed by Forbes (1882a) in the "Oligomyodae" (the Tyrannoidea of later writers) solely on the basis of the insertion of the syringeal muscles. The syrinx shows a unique combination of cartilaginous fusion and lack of intrinsic musculature. These two peculiar genera show no clear relationship to any New World tyrannoid group. Without knowledge of other anatomical and behavioral features, it is unlikely that the true position of the Acanthisittidae can be determined. The patterns of egg-white proteins (Sibley, 1970) support the conclusion that neither the Pittidae nor the Acanthisittidae are closely related to the New World Tyrannoidea.

COTINGIDAE.

The cotingas, as treated by Ridgway, Hellmayr, and most modern systematists, contain two distinct groups with respect to syringeal morphology. The majority of genera, which I have retained in the family as discussed low, lack intrinsic syringeal muscles (except for the bellbirds) and internal cartilages. Most rely on structural and chromatic elaborations of the feathers for species recognition and courtship. The remaining genera, consisting of *Attila, Casiornis, Laniocera, Rhytipterna* and *Iodopleura,* possess oblique ventral intrinsic muscles and internal cartilages, thus resembling the Tyrannidae far more than the typical cotingas. The resemblance to the Tyrannidae is further enhanced by their bill shape, strong rictal bristles, and plain coloration (except for *Iodopleura*). The first four genera are discussed under the Tyrannidae.

The members of the *cotinga* group are medium-sized birds, many strongly colored. Their syrinx is characterized by a small amount of specialization of the lower A-elements and only a slight flare at the region of bifurcation. They possess only a narrow M. tracheolateralis in the syringeal region. In this category are the genera

Cotinga, *Xipholena*, *Heliochera*, *Euchlornis*, and possibly *Tityra*. The last of these genera is often separated as a subfamily, for its members have a number of structural peculiarities, such as the bare facial areas and hooked bills, and unusual behavioral traits, such as their habit of nesting in holes.

In the *Pyroderus* group, sometimes called fruit crows, the lower three to five A-elements are enlarged, divided, and usually individually broadened, overlapping like shingles and creating a broad cavity in the region of bifurcation. By contrast, the B-elements are reduced both in number and in size, resulting in rapidly tapering bronchi of short length. In some of this group the anterior portion of the trachea is enlarged to form a long cavity (*Perissocephalus*, *Cephalopterus*). The fruit crows are the largest of the cotingas, reaching the size of the true crows (*Corvus*). Their colors are more subdued than those of the *Cotinga* group, many being predominantly black. The group includes the genera *Pyroderus*, *Perissocephalus*, *Gymnoderus*, *Conioptilon*, *Gymnocephalus*, and *Cephalopterus*.

The *Querula* group differs only slightly from the last in syringeal structure. The lower A-elements are more strongly arched, creating a more hemispherical cavity. There is no enlargement of the anterior trachea. The simple musculature of the previous two groups is found here also. In this group are *Querula* and *Carpodectes*.

The four species of bellbirds (*Procnias*) have evolved simple, loud, ringing calls, produced by a highly muscular syrinx. The syringeal cartilages and muscles are so specialized that they tell us little about the relationships of *Procnias*.

The cocks-of-the-rock (*Rupicola*) are sometimes given family status, on the basis of their arena courtship behavior and several structural features. The latter include the crest-like frontal feathers (a feature also found in *Phoenicircus*), syndactyly, and homeomery (the dominant artery of the thigh is the sciatic; cf. Garrod, 1876). The presence of syndactyly may be linked to the courtship behavior, for syndactyly occurs in several unrelated birds that utilize vertical perches, as do the cocks-of-the-rock. The simple syrinx of *Rupicola* is much like that of the typical cotingas, representing little adaptation for elaborate vocalizations.

The cotinga genus *Iodopleura* would appear from syringeal structure to be allied to the Tyrannidae, but differs in coloration and beak shape from other members of that family. Determination of the relationships of *Iodopleura* must await the study of other taxonomic characters.

PHYTOTOMIDAE.

The plant-cutters of the genus *Phytotoma* are said to be closely related to the cotingas on account of the simplicity of their syrinx and their tarsal envelope. Certainly there is no other New World group with which the Phytotomidae agree more closely in these two characters. The evident similarity of the syrinx of *Phytotoma* to that of some cotingas (particularly *Heliochera*) may indicate merely that both groups have retained the primitive syringeal structure, as appears to have been the case with the Eurylaimidae and Pittidae. A complete examination of structural and behavioral characters is needed before the systematic position of the Phytotomidae can be determined.

PIPRIDAE.

A close relationship of manakins and cotingas is accepted by most modern systematists, some of whom question whether the two families are really separable. A reliable means of separating the two groups from the Tyrannidae has long been sought. Garrod (1876) used the arteries of the thigh to separate the Pipridae and Cotingidae (except *Rupicola*) from the Tyrannidae. Ridgway (1907) relied strongly on the form of the tarsal envelope and the degree of syndactyly. Hellmayr (1927) reversed many of Ridgway's decisions, using bill shape and wing modifications as accessory criteria. Although too few manakins were available for a complete analysis of syringeal structure, it is evident from the examination of seven genera that considerable variation exists.

Pipra and *Manacus* are very similar in cartilaginous elements, but differ in musculature, *Pipra* possessing intrinsic muscles, *Manacus* none. *Chiroxiphia* shows relationships to *Pipra* in the cartilages and in the general type of intrinsic muscles. *Corapipo* has a peculiar form of musculature, which Garrod might have called "acromyodean," in that the muscles insert on the ends of the elements. The pattern of musculature, however, is quite unlike that of the oscines and the cartilages of *Corapipo* are not greatly different from those of others of the Tyranni. The cartilaginous structure of the syrinx in *Piprites* is reminescent of that in the small tyrannids *Myiobius* and *Terenotriccus*, while the musculature differs only in being narrower. Except for the *Piprites-Myiobius* complex and *Ilicura*, the few manakins examined show little syringeal similarity to the typical members of either the Tyrannidae or Cotingidae.

The thrush-like manakin (*Schiffornis*) differs from other manakins in that its intrinsic musculature is lateral and slightly oblique. The general appearance of its syrinx, with rather simple cartilages and long, straight bronchi, is quite like that of the cotinga *Lipaugus*, but my specimen of the latter is too badly shot damaged to allow close comparison with either *Schiffornis* or the typical cotingas. *Schiffornis* is unique among the manakins that I have studied in possessing internal cartilages, but the manakins are so heterogeneous in syringeal structure that I have come to expect almost anything.

The military manakin (*Ilicura*), with oblique intrinsic muscles and no fusion of A-elements, stands somewhat apart from the "nucleus" of manakins represented by *Pipra*, *Manacus* and *Chiroxiphia*. It is no more divergent from this nucleus than *Corapipo*, *Piprites* and *Schiffornis*, however—all have diverged in different ways—, and only further study will reveal whether or not the tyrannid nature of the syrinx is indicative of the relationships of *Ilicura*.

TYRANNIDAE.

The tyrant flycatchers are the most diverse of suboscine families. Although the "typical" tyrannid could be described as a small olive bird with a flat, slightly hooked bill and strong rictal bristles, there are more atypical forms than typical ones. Usually the tarsus is exaspidean and the toes lack syndactyly (Sclater, 1888). In all of their external characters the Tyrannidae are so variable that taxonomic boundaries and relationships within the family and with other families are often difficult to determine.

With few exceptions the tyrannid syrinx is characterized by the presence of an intrinsic muscle, M. obliquus ventralis, and internal cartilages. Rarely, a second intrinsic muscle, M. obliquus lateralis, is present. Outside the traditional limits of the Tyrannidae (as revised by Hellmayr, 1927) M. obliquus ventralis and internal cartilages occur in New World Tyranni, separately or together, only in *Oxyruncus*, *Corythopis,* the manakin *Ilicura* and a few members of the Cotingidae. The Sharpbill, *Oxyruncus,* has a few distinctive structural features and appears to merit family status. *Corythopis* and the "cotingas" are discussed below in the revised family Tyrannidae.

Among the 86 genera of tyrant flycatchers examined in this study, several structural groups may be distinguished, each with a high degree of syringeal homogeneity and with certain features not found elsewhere in the family. Some groups represent variations of a generalized tyrannid form; others are so specialized as to hide their relationships. The remaining genera have either highly specialized or intermediate syringes, making taxonomic placement difficult. The groups below are not presented as subfamilies, for the descriptions do not include all of the characters on which subfamilies should be based. I have attempted to group together genera which syringeal morphology suggests are most closely related. For ease of reference I am handling each group under the name of a typical genus.

1. The *Fluvicola* group is characterized by: the presence of a dorsal cartilaginous plug, to which the short, usually triangular internal cartilages are attached; extreme development of M. sternotrachealis, which usually inserts with three fasciculi; a short, broad, rather flat M. obliquus ventralis, which inserts on A-1. The nucleus of this group are the genera *Xolmis, Neoxolmis, Agriornis, Muscisaxicola, Fluvicola, Gubernetes, Knipolegus, Muscipipra,* and *Phaeotriccus.*

Lichenops [= *Hymenops*] is probably an offshoot of this group, having evolved a much more robust M. obliquus ventralis and associated cartilages. *Satrapa* and *Entotriccus* probably also belong here, differing from the more typical genera in the form of M. sternotrachealis and in the shape of the internal cartilages. *Lessonia,* which differs from the others of the group in the peculiar dorsal pattern of the A-elements, agrees with them in the musculature.

Although all of the above genera were placed by Hellmayr and his immediate predecessors in the subfamily Fluvicolinae, some genera placed in that subfamily do not appear, from their syringeal structure, to belong near the nucleus of the group. The genera *Ochthoeca* and *Colonia* are similar to each other in several aspects of their syringeal morphology and different from the typical members of the *Fluvicola* group. The phoebes (*Sayornis*) agree more closely in cartilages and musculature, as well as in their external appearance, with members of the *Nuttallornis* group. The Vermillion Flycatcher, *Pyrocephalus,* is strongly unlike the typical members of this group in syringeal musculature, but like them in the cartilages. Müller (1847) noted the similarity of the syringeal musculature of this genus to that of the becards (*Pachyramphus*), but in view of the dissimilarities of the cartilages, I believe the myology to be convergent. I do not feel that the syrinx is of much help in determining the position of *Pyrocephalus.*

Machetornis is unlike the *Fluvicola* group in all aspects of its syringeal structure except the form of M. sternotrachealis. It is possible that the great development of this muscle is in some way linked to a strongly terrestrial existence, in which case a strong M. sternotrachealis would be expected to exist in many unrelated long-legged birds. It is true that very robust Mm. sternotracheales are found in the ground-living antbirds, *Conopophaga*, *Formicarius*, and *Grallaria*, but the mode of insertion of this muscle in the typical antbirds (see *Taraba*, Pl. 3), is more like that of this group of flycatchers. It is not possible to say whether the lack of intrinsic musculature in *Machetornis* is the result of secondary change from a syrinx like that of *Xolmis*, or whether the thick, diffusely attached M. sternotrachealis is convergent, because we do not yet know the functional significance of the various syringeal types.

2. The *Tyrannus* group is syringeally the most homogeneous of the subdivisions. The syrinx is characterized by: close-fitting lower A-elements, usually with ventral fusion; one or more double A-elements, with sharp dorsomedial corners; ventral terminal fusion of two B-elements; short, straight internal cartilages; M. sternotrachealis with diffuse insertion (as in the *Fluvicola* group); short, broad, prominently bulging Mm. obliqui ventrales, which usually do not touch each other at the ventral midline. Of the genera examined in this study, the group includes: *Tyrannus*, *Muscivora*, *Tolmarchus*, *Tyrannopsis*, *Empidonomus*, *Myiodynastes*, *Megarhynchus*, *Conopias*, and *Pitangus* (*sulphuratus* only). *Pitangus* has some cartilaginous modifications which set it apart from the more typical members of the group. *Pitangus lictor* lacks most of the features of the group and, in view of the structural homogeneity found among those listed above, it is difficult to believe *lictor* and *sulphuratus* are more closely related to each other than the latter is to *Tyrannus* and others with which it shares many syringeal features.

All of the above genera were included by Hellmayr (1927) in the subfamily Tyranninae, but interspersed among them were *Legatus*, *Sirystes*, and *Coryphotriccus*. I have not examined the last of these, but the other two do not appear to belong in the middle of the *Tyrannus* group in a linear arrangement, since they lack almost all of the syringeal features listed above. *Legatus* seems to be most like *Myiozetetes* in syringeal musculature, but the two are different in several aspects of the cartilages. The syrinx does not indicate much about their position within the family. The systematic position of *Sirystes* has always been uncertain. Ridgway (1907, p. 339) placed it in the Cotingidae, primarily on the basis of its holaspidean tarsus. Hellmayr (1927) placed it in the Tyrannidae without comment, a course followed by most recent authors. The syrinx of *Sirystes* is typically tyrannid in cartilages and musculature with little similarity to the simple syringes of the Cotingidae as restricted above, but its syrinx resembles those of the *Fluvicola* group more than those of the *Tyrannus* group and bears little resemblance to those of the becards (*Pachyramphus*).

3. The *Nuttallornis* group is closest to the *Fluvicola* group in syringeal structure. The most characteristic feature of the syrinx is complete or partial continuity between the Mm. obliqui ventrales. This condition reaches the extreme in *Sayornis*, in which the superficial muscle layer of some specimens is wholly continuous, having essentially two insertions and no origin. In those genera lacking fiber continuity across the ventral midline, the Mm. obliqui ventrales originate on a median raphe, not, as in the *Fluvicola* and *Tyrannus* groups, directly on the ventral surfaces of the cartilages. In

most members of the *Nuttallornis* group M. tracheolateralis extends beneath the oblique muscle to insert on A-1 or A-2. The group includes *Nuttallornis*, *Sayornis*, *Myiochanes* [= *Contopus*], *Blacicus*, *Empidonax*, *Aechmolophus*, *Aphanotriccus*, and possibly *Muscigralla*.

The last genus deserves special comment, for some authors have considered it out of place in the Tyrannidae. *Muscigralla* is a very unlikely tyrannid, but its syrinx strongly supports its inclusion in the family. Ridgway (1907, p. 339), noting its holaspidean tarsi, felt that it "probably belongs in the Formicariidae," despite the fact that by his own definition the Formicariidae have taxaspidean tarsi. Hellmayr (1927) included *Muscigralla* in the Tyrannidae, but called it "a bird of doubtful affinities," which "probably belongs in another family." The lack of "tracheophone" features in the syrinx excludes *Muscigralla* from the Furnarii, while the presence of M. obliquus ventralis and internal cartilages supports its inclusion in the Tyrannidae. I have placed it near the *Nuttallornis* group because the musculature of the syrinx agrees closely with that of other members of the group.

4. The *Myiobius* group consists of four genera placed by Hellmayr (1927) in the subfamily Myiarchinae with all of the *Nuttallornis* group. Characteristic of the syringes of this group, which includes *Myiobius*, *Terenotriccus*, *Pyrrhomyias* and *Onychorhynchus*, are the possession of two double A-elements and the absence of intrinsic muscles. The four genera seem to be more closely related to each other than to the *Nuttallornis* group, which appears from external characters to contain their closest relatives. The manakin *Piprites* probably also belongs here.

5. The *Myiarchus* group contains some genera placed by Hellmayr (1927) and most other authors in the Cotingidae. The group includes *Myiarchus*, *Eribates*, *Attila*, *Casiornis*, *Laniocera*, and *Rhytipterna*. In all of these the syrinx is characterized by broad ventral Mm. tracheolaterales with little or no midventral space between the pair; narrow Mm. sternotracheales; the Mm. obliqui ventrales attached directly (without a raphe) midventrally and on one or more A-elements laterally; narrow J- or ⅃-shaped dorsal internal cartilages; a smaller ventral pair of internal cartilages. Several of these features occur elsewhere in the Tyrannidae, but only the above genera are known to possess all of them.

The transfer of *Attila* to the Tyrannidae has been suggested by several authorities. Ridgway (1907, p. 770), while retaining *Attila* in the Cotingidae, noted that, along with *Lipaugus*, *Casiornis*, *Sirystes*, and *Tolmarchus*, *Attila* was "essentially if not typically taxaspidean," differing from the majority of cotingas. Hellmayr (1927) remarked that *Attila* "should probably be included among the Tyrannidae." He felt that "in spite of its exaspidean tarsus and cohesion of the toes," *Laniocera* belonged "with *Lipaugus* and *Rhytipterna*, and not with the Pipridae." Apparently he did not consider the possibility that *Laniocera* and *Rhytipterna* might be tyrannid. Zimmer (1936), in describing the new genus *Pseudattila* said that "whether this genus [*Pseudattila*] belongs in the Tyrannidae or in the Cotingidae must await study of internal features. The genus *Attila* is in like predicament."

In external appearance most species of *Attila* are far more like the Tyrannidae than the Cotingidae. They are plain-colored, sexually monomorphic, and primarily insectivorous. The bill is broad at the base and strongly hooked at the tip. *Casiornis*. *Laniocera*, and *Rhytipterna* exhibit these tyrannid characters less strongly, but their outward appearance suggests tyrannid affinities. *Lipaugus* may later be added to this group. The damaged specimen examined by me and the specimen studied by Garrod (1877b) seem to differ regarding M. obliquus ventralis and internal cartilages, but further examination is needed before the syringeal structure will be thoroughly known.

The similarity of the syrinx of the four "cotingas" listed above to that of *Myiarchus* is striking. Without assuming strong interdependence of several syringeal features, it is difficult to see how two groups of birds could evolve both external and internal similarities to such a degree.

The structure of the myiarchine syrinx does not provide many clues to the relationships of the group within the family. Externally their appearance suggests that their closest relatives might lie in the *Tyrannus* group.

6. The *Colopteryx* group have several features of the syrinx that are not found elsewhere. The most striking are the long dorsal extension of the pessulus, accompanied by dorsally incomplete elements, and the long, narrow, overlapping Mm. obliqui ventrales. These two features may well be funtionally interdependent. The group contains *Colopteryx, Oncostoma, Euscarthmornis, Hemitriccus, Myiornis,* and *Lophotriccus,* all of which were placed by Hellmayr in the Euscarthminae. In his linear arrangement no genera examined in this study were placed among the six above.

The flatbills, *Platyrinchus,* have a small mid-dorsal plate (but no pessulus) and long but not crossed Mm. obliqui ventrales, suggesting that they might belong in or near the *Colopteryx* group. The Mm. tracheolaterales extend further posteriad than in the *Colopteryx* group. Von Ihering (1904) believed *Platyrinchus* to be closely related to *Oncostoma* and *Hemitriccus*, a view supported by von Berlepsch (1905). Hellmayr (1927) restricted the subfamily Platyrinchinae to the flat-billed forms, *Cnipodectes, Tolmomyias, Rhynchocyclus, Platyrinchus*, and *Ramphotrigon.* I have not been able to obtain specimens of *Cnipodectes* and *Ramphotrigon* but the other three differ so strongly in their syringeal structure that one may seriously question the reliability of bill shape as a common character for the five genera.

Tolmomyias sulphurescens and *T. megacephalus* differ strikingly in syringeal cartilages and musculature. Zimmer (1939) transferred *megacephalus* to the genus *Ramphotrigon,* largely on the basis of coloration. The transfer of *megacephalus* out of *Tolmomyias,* at least, is supported by the syringeal morphology.

7. In the *Elaenia* group the syrinx is characterized by the presence of a well-fused drum and of M. obliquus lateralis. In most forms the well-developed M. obliquus ventralis originates on a median raphe attached to the drum. The internal cartilages are narrow curved bars, usually with flat ventral extensions. Included are *Elaenia, Suiriri, Camptostoma, Tyrannulus,* and *Phaeomyias.*

Elaenia gaimardi was moved from the Tyrannidae to the Pipridae by Ridgway (1905), solely on the basis of its pycnaspidean tarsus and basal syndactyly. He made it the type of a new genus *Elainopsis.* The new genus was not recognized by most subsequent authors, who have retained *gaimardi* in *Elaenia* or in *Myiopagis.* The latter genus was erected by Salvin and Godman (1888) for certain forms with specialized nostrils. The relative uniformity of syringeal structure among the nine species of *Elaenia* examined supports Hellmayr's (1927) contention that *Elaenia* is "a very natural genus."

The genera *Microtriccus* and *Tyranniscus* (perhaps only *nigrocapillus*) probably belong near the *Elaenia* group. Ridgway (1907, p. 339) transferred *Microtriccus*

[=*Ornithion*] along with *Tyrannulus*, to the Cotingidae on the basis of their pycnaspidean tarsi, but Hellmayr (1927) and most recent authors have retained both in the Tyrannidae. The syringeal cartilages of *Microtriccus* fit the *Elaenia* pattern closely, with a fully fused drum and flat extensions on the internal cartilages. *Microtriccus* differs from the *Elaenia* group in lacking M. obliquus lateralis. There is little to suggest whether *Microtriccus* diverged from the *Elaenia* line before the appearance of the lateral muscle or whether the muscle was lost secondarily. *Tyrannulus* has a suggestion of M. obliquus lateralis in the deep dorsal fibers of M. obliquus ventralis, the direction of which is different from that of the superficial fibers. More specimens of *Tyrannulus* are needed to determine the extent of individual variation in this muscle.

The two species of *Tyranniscus* examined differ so strikingly in syringeal morphology that I felt it necessary to verify the identity of the specimens through comparison with skins. One cannot help wondering if a thorough analysis of structural and behavioral characters of these and other species of *Tyranniscus* would not result in dividing the genus.

8. The syringeal morphology of the following genera does not provide much indication of their position within the Tyrannidae, but affects their family allocation, which has sometimes been questioned.

Euscarthmus. Ridgway (1907, p. 339), treating this genus as *Hapalocercus*, believed that it was "probably . . . formicarian in its affinities," largely on the basis of its taxaspidean tarsal envelope. Wetmore (1926) felt that *Euscarthmus* was "certainly not a true flycatcher," and placed the genus tentatively in the antbirds. Hellmayr (1927, p. 357) echoed Ridgway's remarks and called the position of *Euscarthmus* "quite uncertain," although he placed it in the Tyrannidae. The genus does not agree with any of the Furnarii in its syringeal structure, but does fit easily into the Tyrannidae. Its long, anteriorly situated drum and long, narrow internal cartilages are unlike those of any other genus that I have examined. In syringeal musculature *Euscarthmus* resembles *Inezia* and *Pogonotriccus*, but the similarities are not strong and all three have simple Mm. obliqui ventrales.

Stigmatura. This genus was placed by Ridgway (1907, p. 339) in the Formicariidae on the basis of its resemblance "in general form" to the antbird genus *Formicivora* [=*Neorhopias*], and Wetmore (1926) agreed with Ridgway's allocation of the genus. Hellmayr (1927, p. 379) included *Stigmatura* in the Tyrannidae, but suggested that it might belong in the Formicariidae. *Stigmatura* is typically tyrannid in its syrinx, with no resemblance to the Furnarii.

Habrura. Ridgway (1907, p. 339) felt that *Habrura* could not be a tyrannid and "might not be out of place in the Cotingidae," basing his opinion on the shape of the nostrils and the configuration of the tarsal envelope. Most other authorities have retained this genus in the Tyrannidae, although Hellmayr expressed skepticism that it belonged there. The syringeal structure of *Habrura* supports its inclusion in the Tyrannidae, but its placement within the family is not greatly aided by syringeal morphology. In the shape of the intrinsic muscles *Habrura* most resembles *Capsiempis* but the cartilages of both genera are of a type widely distributed in the family.

Mionectes and *Pipromorpha*. The peculiar syringeal structure of these two genera, with very small, ventrally located Mm. obliqui ventrales and extensive fusion of the lower A-elements, is unlike other members of Hellmayr's subfamily Elaeniinae. The posterior ventral narrowing of the Mm. tracheolaterales probably cannot be taken as indicating relationships, for it occurs in others of the family, apparently unrelated to *Mionectes* and *Pipromorpha,* namely *Pachyramphus, Pyrocephalus* and *Colorhamphus.* The syringes of *Pipromorpha* and *Mionectes* are identical, considered in the light of the variability in the rest of the family, and support the merger of the two genera suggested by Todd (1921) and Hellmayr (1927).

Corythopis. This interesting genus of "ant-pipits," usually placed with *Conopophaga* in the family Conopophagidae, has been found (Ames et al., 1968) to be unrelated to the antbird-ovenbird assemblage and to be typically tyrannid in several features of its anatomy. The syrinx of *Corythopis* is notable for the peculiar shape of the internal cartilages, which are not far from those of *Leptotriccus sylveolus.* There is little in the external anatomy to suggest a relationship between the two genera, so one may probably assume the slight similarity of internal cartilages to be convergent.

Pachyramphus and *Platypsaris.* The becards have been placed in the Cotingidae by all authors and I know of no one who has suggested that they might be tyrannid. Müller (1847) noticed the resemblance in syringeal musculature between *Pachyramphus rufus* and *Pyrocephalus rubinus,* but the resemblance does not extend to the cartilages. Suffice to say, the becards have several tyrannid features of the syrinx that are not found in the more typical members of the Cotingidae. Moreover they are plain-colored, only slightly sexually dimorphic, and primarily insectivorous. It is likely that a thorough investigation of many unrelated taxonomic characters would show that the becards are more closely related to the Tyrannidae than to *Cotinga, Pyroderus,* and others of the restricted family Cotingidae.

OXYRUNCIDAE.

The peculiar sharpbill (*Oxyruncus cristatus*) has a basically tyrannid syrinx, with oblique ventral intrinsic muscles and internal cartilages, but I cannot agree with Clark (1913) that its syrinx bears a "striking resemblance" to that of any particular genus of tyrannid, least of all to *Tyrannus* and *Sayornis.* The syringeal musculature of the sharpbill is strikingly like that of the becards (*Pachyramphus*) but there are substantial differences in the supporting cartilages. The type of musculature found in the sharpbill and the becards occurs elsewhere among the Tyrannidae, so the similarity should not be given too much weight.

MENURAE.

The lyrebirds (*Menura*) and scrub-birds (*Atrichornis*) are currently separated from the suborder Passeres primarily on the basis of their smaller number of syringeal muscles and the peculiarities of their pectoral apparatus and flight feathers. The lyrebirds and scrub-birds are more alike in syringeal structure than was previously inferred from the work of Garrod (1876), who reported finding only two pairs of intrinsic muscles in *A. rufescens*. It is possible that the two species of *Atrichornis* differ in the number of syringeal muscles, but I am inclined to believe that Garrod overlooked a pair of muscles. Although the musculature is very close to the oscine pattern, there are major differences in the cartilages. In both muscles and cartilages, the Menurae lie well outside the range of variation shown by the vast array of recognized oscines. The syringeal evidence supports the osteological and pterylographic characters in separating the Menurae from the Passeres.

PASSERES OR "OSCINES".

The extreme homogeneity of the oscine syrinx strongly supports the present inclusion of the fifty-odd families in a single suborder. Detailed comment on the taxonomic relationships of the various families is beyond the scope of this paper, but some remarks on the supposed primitiveness of the syrinx in the larks and swallows are appropriate. No single group of oscines can be considered syringeally primitive, in the sense that the Menurae can be considered so. The features that distinguish the syrinx in the Alaudidae (absence of the pessulus) and Hirundinidae (double bronchial elements) were almost certainly not found in the syrinx of the ancestral oscine and must be considered adaptive modifications of unknown value. Although the larks and swallows do represent distinct and probably early offshoots of the main oscine stem, a contention supported by their syringeal structure and a number of other characters, the term "primitive" is inappropriate as applied to their syrinx.

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APPENDIX A

DATA FOR SPECIMENS OF THE SUBORDERS EURYLAIMI, FURNARII, TYRANNI AND MENURAE

In this appendix are listed the available data for all of the suboscine specimens examined in this study. The nomenclature and taxonomic order are drawn from the following sources: Eurylaimi, Peters (1951); Furnarii and Tyranni (New World families), Hellmayr (1924-28); Pittidae, Smythies (1940, 1960) and Mackworth-Praed and Grant (1955); Philepittidae, Rand (1936) and Amadon (1951); Acanthisittidae, Flemming (1953); Menurae, Cayley (1931).

Abbreviations

The institutions from which the specimens were obtained are indicated by the following abbreviations:

AMNH	American Museum of Natural History, New York, New York.
BM	British Museum (Natural History), London.
CM	Carnegie Museum, Pittsburgh, Pennsylvania
LSUMZ	Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana.
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley, California.
USNM	United States National Museum, Washington, D. C.
WGG	William G. George Collection. Southern Illinois University, Carbondale, Illinois.
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Suborder Eurylaimidae

FAMILY EURYLAIMIDAE. BROADBILLS.

Smithornis capensis (A. Smith)	YPM 1608; Tanganyika; Sep 1961; Coll: G. H. Heinrich.
Smithornis rufolateralis G. R. Gray	AMNH (no number); Congo; 7 Sep 1930; Coll: J. P. Chapin.
Cymbirhynchus macrorhynchus (Gmelin)	USNM 290033; Sumatra; 1921; Coll: H. C. Keller.
Eurylaimus javanicus Horsfield	USNM 290082; Sumatra; 1921; Coll: H. H. Keller.
Serilophus lunatus (Gould)	USNM 439900; Thailand; 24 May 1955; Coll: R. E. Elbel.
Psarisomus dalhousei (Jameson)	USNM 429906; Borneo; 2 Aug 1953; Coll: R. Traub.
Calyptomena whiteheadi Sharpe	USNM 429241; Borneo; 1953; Coll: R. E. Elbel.

Suborder Furnarii

FAMILY DENDROCOLAPTIDAE. WOODCREEPERS.

Dendrocincla fuliginosa (Vieillot)	YPM 1017; Colombia, Magdalena; 21 May 1961; Coll: M. A. Carriker, Jr.
Sittasomus griseicapillus (Vieillot)	AMNH (no number); Brazil; 1 Mar 1930; Coll: E. Kaempfer.
Glyphorhynchus spirurus (Vieillot) ♀	YPM 1071; Colombia, Magdalena; 8 Apr 1961; Coll: M. A. Carriker, Jr.
Glyphorhynchus spirurus (Vieillot) ♂	YPM 1802; Surinam; 26 Nov 1961; Coll: R. Freund.
Drymornis bridgesii (Eyton)	USNM 227568; Argentina, Victoria; 23 Dec 1920; Coll: A. Wetmore.
Xiphocolaptes promeropirhynchus (Lesson)	YPM 2089; Colombia, Santander; 10 Jan 1962; Coll: M. A. Carriker, Jr.
Xiphocolaptes major (Vieillot)	AMNH (no number); Brazil; date unknown; Coll: E. Kaempfer.
Dendrocolaptes platyrostris Spix	YPM 2284; Argentina, Misiones; 7 Jul 1961; Coll: P. S. Humphrey.
Xiphorhynchus picus (Gmelin)	YPM 2040; Colombia, Santander; 17 Apr 1962; Coll: M. A. Carriker, Jr.
Xiphorhynchus picus (Gmelin)	AMNH (no number); Brazil; 4 Apr 1963; Coll: E. T. Gilliard.
Lepidocolaptes souleyetii (Des Murs)	YPM 1022; Colombia, Magdalena; 24 May 1961; Coll: M. A. Carriker, Jr.
Lepidocolaptes affinis (Lafresnaye)	YPM 2058; Colombia, Santander; 4 Jan 1962; Coll: M. A. Carriker, Jr.
Lepidocolaptes albolineatus (Lafresnaye)	YPM 1813; Surinam; 3 Dec 1961; Coll: R. Freund.
Campylorhamphus trochilirostris (Lichtenstein) ♀	YPM 2277; Argentina, Misiones; 16 June 1961; Coll: P. S. Humphrey.

FAMILY FURNARIIDAE. OVENBIRDS.

Geositta cunicularia (Vieillot) ♀	YPM 3823; Argentina, Sta. Cruz; 11 Jan 1961; Coll: P. S. Humphrey.
Geositta cunicularia (Vieillot) ♂	YPM 3825; Argentina, Sta. Cruz; 11 Jan 1961; Coll: P. S. Humphrey.
Geositta cunicularia (Vieillot)	YPM 18; Chile; 1958; Coll: L. E. Peña.
Furnarius leucopus Swainson	AMNH (no number); Brazil; no other data.
Cinclodes patagonicus (Gmelin) ♀	YPM 2326; Argentina, Sta. Cruz; 1 Dec 1960; Coll: P. S. Humphrey.
Cinclodes patagonicus (Gmelin) ♂	YPM 2327; Argentina, Sta. Cruz; 1 Dec 1960; Coll: P. S. Humphrey.
Cinclodes fuscus (Vieillot)	YPM 2846; Argentina, Sta. Cruz; 26 Dec 1960; Coll: P. S. Humphrey.
Upucerthia dumetaria Geoff. St. Hilaire	YPM 3833; Argentina; 14 Jan 1961; Coll: P. S. Humphrey.
Limnornis curvirostris Gould	AMNH (no number); Brazil; no other data.
Aphastrura spinicauda (Gmelin)	YPM 9; Chile, Santiago; 20 Aug 1958; Coll: L. E. Peña.
Phleocryptes melanops (Vieillot)	YPM 2542; Argentina, Entre Rios; 1 Apr 1961; Coll: P. S. Humphrey.
Phleocryptes melanops (Vieillot)	AMNH (no number); Brazil; no other data.

Synallaxis cinerascens Temminck	YPM 2547; Argentina, Misiones; 11 Jul 1961; Coll: P. S. Humphrey.
Certhiaxis cinnamomea (Gmelin)	CM 65; Venezuela, Guarico; 10 Sep 1927; Coll: E. G. Holt.
Asthenes pyrrholeuca (Vieillot) ♂	YPM 2364; Argentina, Chubut; 19 June 1961; Coll: P. S. Humphrey
Phacellodomus rufifrons (Wied)	AMNH (no number); Brazil; no other data.
Phacellodomus striaticollis (Lafr. and D'Orb.)	YPM 2374; Argentina, Entre Rios; 30 Apr 1961; Coll: P. S. Humphrey.
Anumbius anumbi (Vieillot)	YPM 2304; Argentina, Buenos Aires; 28 Oct 1960; Coll: P. S. Humphrey.
Pseudocolaptes boissoneautii (Lafr.)	YPM 2088; Colombia, Santander; 9 Jan 1962; Coll: M. A. Carriker, Jr.
Pseudoseisura lophotes (Reichenbach)	YPM 2397; Argentina, Rio Negro; 12 Feb 1961; Coll: P. S. Humphrey.
Pseudoseisura gutteralis (Lafr. and D'Orb.) ♂	YPM 2409; Argentina, Chubut; 16 Jan 1961; Coll: P. S. Humphrey.
Anabazenops fuscus (Vieillot)	AMNH (no number); Brazil, Sta. Catarina; no other data.
Philydor rufus (Vieillot)	AMNH (no number); Brazil; no other data.
Automolus ochrolaemus (Tschudi)	AMNH (field no.) 726; Nicaragua; 1917; Col: W. deW. Miller.
Heliobletus contaminatus Berlepsch	AMNH (no number); no data.
Xenops minutus (Sparrman)	YPM 1042; Colombia, Santander; 10 Mar 1961; Coll: M. A. Carriker, Jr.
Megaxenops parnaguae Reiser	AMNH (field no.) 6113; Brazil, Bahia; 12 Aug 1927; Coll: E. Kaempfer.
Pygarrhicus albogularis (King)	YPM 56; Chile, Malleco; 30-31 Dec 1958; Coll: L. E. Peña.
Sclerurus guatemalensis (Hartlaub)	USNM 431001; Panamá; 6 Mar 1959; Coll: unknown.

FAMILY FORMICARIIDAE. ANTBIRDS.

Cymbilaimus lineatus (Leach) ♂	AMNH (field no.) 750; Nicaragua; 1917; Coll: W. deW. Miller.
Cymbilaimus lineatus (Leach) ♀	AMNH (field no.) 764; Nicaragua; 1917; Coll: W. deW. Miller
Hypoedaleus guttatus (Vieillot)	YPM 2650; Argentina; Misiones; 12 Feb 1961; Coll: P. S. Humphrey.
Taraba major (Vieillot) ♂	AMNH (field no.) 765; Nicaragua; 1917; Coll: W. deW. Miller
Sakesphorus canadensis (Linnaeus)	AMNH (no number); British Guiana; "10/12/37;" Coll: R. Snediger.
Thamnophilus doliatus (Linnaeus) ♀	YPM 1055; Colombia, Santander; 22 Mar 1961; Coll: M. A. Carriker, Jr.
Thamnophilus doliatus (Linnaeus) ♀	AMNH (no number); Nicaragua; 1913; Coll: W. deW. Miller.
Thamnophilus punctatus (Shaw)	AMNH (field no.) 738; Nicaragua; 1917; Coll: W. deW. Miller
Thamnophilus punctatus (Shaw)	YPM 999; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Thamnophilus punctatus (Shaw)	YPM 1000; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Thamnophilus caerulescens Vieillot	YPM 2497; Argentina, Corrientes; 18 May 1961; Coll; P. S. Humphrey.
Pygiptila stellaris (Spix)	USNM 319838; Brazil, Amazonas; 12 Jan 1931; Coll: E. G. Holt.

Dysithamnus mentalis (Temminck)	YPM 1675; Colombia, Santander; 27 Jul 1961; Coll: M. A. Carriker, Jr.
Dysithamnus mentalis (Temminck)	YPM 1676; Colombia, Santander; 27 Jul 1961; Coll: M. A. Carriker, Jr.
Thamnomanes caesius (Temminck)	AMNH (no number); Brazil, Espirito Santo; 3 Nov 1929; Coll: E. Kaempfer.
Myrmotherula cherriei Berl. and Hart. ♀	USNM 318733; Venezuela, Ter. Fed. Amaz.; 4 Jan 1930; Coll: E. G. Holt.
Myrmotherula axillaris (Vieillot)	USNM 318722; Venezuela, Ter. Fed. Amaz.; 3 Jan 1930; Coll: E. G. Holt.
Myrmotherula axillaris (Vieillot)	YPM 1013; Colombia, Magdalena; 21 May 1961; Coll: M. A. Carriker, Jr.
Myrmotherula axillaris (Vieillot)	YPM 1014; Colombia, Magdalena; 22 May 1961; Coll: M. A. Carriker, Jr.
Herpsilochmus pileatus (Litchtenstein)	AMNH (no number); Brazil, Bahia; 5 May 1928; Coll: W. deW. Miller.
Microrhopias quixensis (Cornalia)	AMNH (field no.) 806; Nicaragua; 1917; Coll: W. deW. Miller.
Neorhopias grisea (Boddaert)	AMNH (no number); Brazil, Bahia; 3 May 1928; Coll: E. Kaempfer.
Neorhopias rufa (Wied)	YPM 1862; Surinam; 10 Dec 1961; Coll: R. Freund.
Drymophila squamata (Lichtenstein)	AMNH (no number); Brazil; date unknown; Coll: E. Kaempfer.
Cercomacra tyrannina (Sclater) ♂	AMNH (field no.) 829; Nicaragua; 1917; Coll: W. deW. Miller.
Cercomacra tyrannina (Sclater) ♂	AMNH (field no.) 830; Nicaragua; 1917; Coll: W. deW. Miller.
Pyriglena leucoptera (Vieillot)	AMNH (no number); Brazil, Bahia; 22 Jun 1926; Coll: E. Kaempfer.
Hypocnemis flavescens (Sclater)	USNM 319828; Brazil; 21 Nov 1930; N. G. S. Brazil-Venez. Exp.
Hypocnemoides melanopogon (Sclater)	USNM 318724; Venezuela, Bolivar; 30 Dec 1929; Coll: E. G. Holt.
Myrmeciza exsul Sclater	YPM 1001; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Myrmoderus squamosus (Pelzeln)	AMNH (no number); Brazil; date unknown; Coll: E. Kaempfer.
Formicarius analis (Lafr. and D'Orb.)	AMNH (no number); Nicaragua; 12 May 1917; Coll: W. deW. Miller
Formicarius analis (Lafr. and D'Orb.)	YPM 987; Colombia, Magdalena; 15 May 1961; Coll: M. A. Carriker, Jr.
Formicarius analis (Lafr. and D'Orb.)	YPM 988; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Formicarius analis (Lafr. and D'Orb.)	YPM 2120; Mexico, Oaxaca; 17 Mar 1962; Coll: W. J. Schaldach, Jr.
Chamaeza brevicauda (Vieillot) ♀	YPM 2457; Argentina, Corrientes; 20 May 1961; Coll: P. S. Humphrey.
Pithys albifrons (Linnaeus)	AMNH (no number); British Guiana; 1927; Coll: A. Lang.
Gymnopithys bicolor (Lawrence)	USNM 225008; Panamá; date unknown; Coll: E. A. Goldman.
Hylophylax naevioides (Lafresnaye) ♂	AMNH (no number); Nicaragua; 1913; Coll: W. deW. Miller.
Hylophylax naevioides (Lafresnaye) ♀	AMNH (field no.) 751; Nicaragua; 1917; Coll: W. deW. Miller.
Grallaria varia (Boddaert)	YPM 2475; Argentina, Corrientes; 12 May 1961; Coll: P. S. Humphrey.
Grallaria perspicillata Lawrence	YPM 1002; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Grallaria perspicillata Lawrence ♂	YPM 1068; Colombia, Magdalena; 3 Apr 1961; Coll: M. A. Carriker, Jr.

Grallaria ochroleuca (Wied)	YPM 2476; Argentina, Misiones; 2 Jul 1961; Coll: P. S. Humphrey.
Conopophaga lineata (Wied)	AMNH (no number); Brazil; date unknown; Coll: E. Kaempfer.
Conopophaga lineata (Wied) ♂	YPM 2550; Argentina, Corrientes; 10 May 1961; Coll: P. S. Humphrey.
Conopophaga lineata (Wied)	YPM 2551; Argentina, Corrientes; 10 May 1961; Coll: P. S. Humphrey.
Conopophaga lineata (Wied)	YPM 2552; Argentina, Corrientes; 10 May 1961; Coll: P. S. Humphrey.
Conopophaga roberti Hellmayr	USNM 195100; Brazil, Pará; June 1963; Coll: P. S. Humphrey.
Conopophaga roberti Hellmayr	USNM 195954; Brazil, Pará; Jun 1963; Coll: P. S. Humphrey.
Conopophaga roberti Hellmayr	USNM 196021; Brazil, Pará; Jun 1963; Coll: P. S. Humphrey.

FAMILY RHINOCRYPTIDAE. TAPACULOS.

Pteroptochos tarnii (King)	YPM 2566; Argentina, Rio Negro; 2 Feb 1961; Coll: P. S. Humphrey.
Pteroptochos tarnii (King)	YPM 2569; Argentina, Rio Negro; 2 Feb 1961; Coll: P. S. Humphrey.
Pteroptochos megapodius Kittlitz	YPM 63; Chile; 1958; Coll: I. E. Peña.
Scelorchilus rubecula (Kittlitz)	YPM 53; Chile, Malleco; 23 Jan 1959; Coll: L. E. Peña.
Rhinocrypta lanceolata (Geoff. Saint Hilaire)	USNM 227619; Argentina; 25 Nov 1920; Coll: A. Wetmore.
Rhinocrypta lanceolata (Geoff. Saint Hilaire)	YPM 2570; Argentina, Rio Negro; 12 Feb 1961; Coll: P. S. Humphrey.
Teledromas fuscus (Scl. and Salv.) ad ♂	USNM 227597; Argentina, Gen. Roca; 25 Nov 1920; Coll: A. Wetmore.
Melanopareia maximilliani (D'Orbigny)	USNM 227944; Argentina, Tucumán; 17 Apr 1921; Coll: A. Wetmore.
Scytalopus magellanicus (Gmelin)	YPM 52; Chile; 1958; Coll: L. E. Peña.
Triptorhinus paradoxus (Kittlitz)	YPM 69; Chile, Maulé; Jan 1959; Coll: L. E. Peña.

Suborder Tyranni

FAMILY COTINGIDAE. COTINGAS.

Phoenicircus carnifex (Linnaeus) ♀	USNM (field no.) 198735; Brazil, Para, Belem; 4 Sep 1964; Coll: P. S. Humphrey.
Heliochera rubrocristata (Lafr. and D'Orb.)	New York Zool. Soc.; no data; Coll: C. W. Beebe.
Cotinga amabilis Gould	YPM 2127; Mexico, Oaxaca; 21 Mar 1962; Coll: W. J. Schaldach, Jr.
Cotinga maculata (Müller)	New York Zool. Soc.; no data; Coll: C. W. Beebe.
Xipholena punicea (Pallas)	AMNH (no number); British Guiana; 2 Feb 1923; Coll: Lang and Varr.
Carpodectes nitidus Salvin	USNM 19845; Costa Rica; 28 Mar 1905; Coll: R. Ridgway.
Euchlornis jucunda (Sclater) ♂	YPM 319; Ecuador; 1 Jan 1958; Coll: M. Erlanger.
Euchlornis aureopectus (Lafresnaye)	AMNH (no number); cage bird; 2 May 1938; New York Zool. Soc.

Euchlornis aureopectus (Lafresnaye)	YPM 2076; Colombia, Santander; 8 Jan 1962; Coll: M. A. Carriker, Jr.
Iodopleura isabellae (Shaw and Nodder)	MCZ (no number); Brazil, Para, Belem; Aug 1961; Coll: J. Hidasi.
Attila spadiceus (Gmelin)	YPM 2130; Mexico, Oaxaca; 21 Mar 1962; Coll: W. J. Schaldach, Jr.
Attila spadiceus (Gmelin)	AMNH (field no.) 866; Nicaragua; 1917; Coll: W. deW. Miller.
Attila cinnamomeus (Gmelin) ♀	USNM (field no.) 198365; Brazil, Para, Belem; 13 Aug 1964; Coll: P. S. Humphrey.
Casiornis rufa Vieillot	USNM 227189; Argentina, Chaco; 21 Jul 1920; Coll: A. Wetmore.
Laniocera rufescens (Sclater)	YPM 986; Colombia, Santander; 16 May 1961; Coll: M. A. Carriker, Jr.
Rhytipterna holerythra (Scl. and Salv.)	YPM 1074; Colombia, Magdalena; 8 Apr 1961; Coll: M. A. Carriker, Jr.
Rhytipterna holerythra (Scl. and Salv.)	YPM 1092; Colombia, Magdalena; 8 Apr 1961; Coll: M. A. Carriker, Jr.
Rhytipterna holerythra (Scl. and Salv.) ♂	AMNH (field no.) 743; Nicaragua; 1917; Coll: W. deW. Miller.
Lipaugus unirufus Sclater	YPM 1005; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Pachyramphus rufus (Boddaert)	YPM 863; Colombia, Santander; 24 Jan 1961; Coll: M. A. Carriker, Jr.
Pachyramphus polychopterus (Vieillot)	YPM 1041; Colombia, Santander; 10 May 1961; Coll: M. A. Carriker, Jr.
Pachyramphus polychopterus (Vieillot)	AMNH (no number); Nicaragua; 1917; Coll: W. deW. Miller.
Pachyramphus viridis (Vieillot)	YPM 2577; Argentina, Misiones; 2 Jul 1961; Coll: P. S. Humphrey.
Platypsaris aglaiae (Lafresnaye) ad ♀	YPM 1531; Mexico, Vera Cruz; 1962; Coll: R. W. Dickerman.
Platypsaris aglaiae (Lafresnaye) ad ♀	AMNH (field no.) 1174; Nicaragua; 1917; Coll: W. deW. Miller.
Platypsaris aglaiae (Lafresnaye)	AMNH (field no.) 1160; Nicaragua; 1917; Coll: W. deW. Miller.
Tityra semifasciata (Spix) ♀	YPM (no number); Mexico, Campeche; 16 Jul 1962; Coll: T. E. Lovejoy.
Tityra inquisitor (Lichtenstein)	YPM 2579; Argentina, Misiones; 21 Jun 1961; Coll: P. S. Humphrey.
Tityra cayana (Linnaeus)	YPM 1817; Surinam; 3 Dec 1961; Col: R. Freund.
Querula purpurata (Müller)	USNM 343943; Panamá; 15 Apr 1937; Col: W. deW. Miller.
Pyroderus scutatus (Shaw) ♂	YPM 3608; Argentina, Misiones; 7 Jul 1961; Coll: P. S. Humphrey.
Pyroderus scutatus (Shaw)	USNM 321594; no data.
Cephalopterus ornatus Geoff. Saint Hilaire	USNM 19802; Costa Rica; 1 May 1905; Coll. R. Ridgway.
Perissocephalus tricolor (Müller)	AMNH (no number); Venezuela; 8 Feb 1938; Coll: W. Phelps.
Gymnoderus foetidus (Linnaeus)	USNM 32160; no data.
Conioptilon mcilhennyi Lowery and O'Neill ♀	LSUMZ 42871; Peru, Loreto; 21 Mar 1965; Coll: J. P. O'Neill.
Procnias tricarunculata (J. and E. Verreaux)	USNM 413214; Panamá, Bocas del Toro; 17 Jan 1960; Coll: unknown.
Rupicola rupicola (Linnaeus) ad ♂	AMNH (no number); British Guiana; 26 Feb 1961; Coll: E. T. Gilliard.

Rupicola rupicola (Linnaeus)	New York Zool. Soc. (no number); no data; Coll: C. W. Beebe.
Rupicola rupicola (Linnaeus) ♂	YPM (no number); USA, Pennsylvania; captive bird; 10 Apr 1962; Coll: K. C. Parkes.

FAMILY PIPRIDAE. MANAKINS.

Piprites chloris (Temminck)	YPM 2582; Argentina, Misiones; 13 Jun 1961; Coll: P. S. Humphrey.
Pipra mentalis Sclater	YPM 2121; Mexico; Oaxaca; 28 Mar 1962; Coll: W. J. Schaldach, Jr.
Pipra mentalis Sclater ♂	AMNH (field no.) 784; Nicaragua; 1917; Coll: W. deW. Miller.
Pipra erythrocephala (Linnaeus)	YPM 985; Colombia, Magdalena; 16 May 1961; Coll: M. A. Carriker, Jr.
Chiroxiphia lanceolata (Wagler)	USNM 343871; Panamá; 16 Feb 1937; Coll: Miller and Wheeler.
Chiroxiphia caudata (Shaw and Nodder)	YPM 2587; Argentina, Corrientes; 18 May 1961; Coll: P. S. Humphrey.
Chiroxiphia caudata (Shaw and Nodder)	AMNH (no number); Brazil; 22 Sep 1928; Coll: E. Kaempfer.
Ilicura militaris Parzudaki	BM 1936-3-5-1; cage bird; died 11 Mar 1936; Coll: A. Ezra.
Corapipo leucorrhoa (Sclater) ♂	USNM 19938; Costa Rica; 1908; Coll: R. Ridgway.
Manacus vitellinus (Gould)	USNM 343873; Panamá; 20 Feb 1937; Coll: Miller and Wheeler.
Manacus candei (Parzudaki)	YPM 2164; Mexico, Oaxaca; 29 Mar 1962; Coll: W. J. Schaldach, Jr.
Schiffornis virescens (Lafresnaye) ♀	YPM 2603; Argentina Corrientes; 11 May 1961; Coll: P. S. Humphrey.
Schiffornis turdinus (Wied)	AMNH (field no.) 892; Nicaragua; 1917; Coll: W. deW. Miller.
Schiffornis turdinus (Wied) ♂	USNM (field no.) 196400; Brazil, Pará; 2 Jul 1964; Coll: P. S. Humphrey.
Schiffornis turdinus (Wied) ♀	USNM (field no.) 196529; Brazil, Pará; 8 Jul 1964; Coll: P. S. Humphrey.

FAMILY TYRANNIDAE. TYRANT FLYCATCHERS.

SUBFAMILY FLUVICOLINAE.

Agriornis livida (Kittlitz)	YPM 21; Chile, Nagué; Sep 1958; Coll: L. E. Peña.
Agriornis microptera Gould	YPM 2613; Argentina, Chubut; 1 Nov 1960; Coll: P. S. Humphrey.
Xolmis coronata (Vieillot) ♂	YPM 2819; Argentina, Buenos Aires; 26 Oct 1960; Coll: P. S. Humphrey.
Xolmis irupero (Vieillot) ♂	YPM 2823; Argentina, Buenos Aires; 24 Oct 1960; Coll: P. S. Humphrey.
Xolmis pyrope (Kittlitz)	YPM 14; Chile; 1958; Coll: L. E. Peña.
Xolmis pyrope (Kittlitz) ♀	YPM 2832; Argentina, Chubut; 20 Jan 1961; Coll: P. S. Humphrey.
Muscisaxicola albilora Lafresnaye	YPM 2712; Argentina, Chubut; 18 Jan 1961; Coll: P. S. Humphrey.
Muscisaxicola maculirostris Lafr. and D'Orb. ♂	YPM 2856; Argentina, Santa Cruz; 23 Dec 1960; Coll: P. S. Humphrey.

Lessonia rufa (Gmelin)	YPM 10; Chile; 1958; Coll: L. E. Peña.
Neoxolmis rufiventris (Vieillot) ♂	YPM 2736; Argentina, Santa Cruz; 14 Nov 1960; Coll: P. S. Humphrey.
Neoxolmis rufiventris (Vieillot) ♀	YPM 2739; Argentina, Santa Cruz; 12 Jan 1961; Coll: P. S. Humphrey.
Ochthoeca fumicolor Sclater	AMNH (field no.) 692; Peru; no other data; Coll: E. Heller.
Ochthoeca fumicolor Sclater	YPM 973; Colombia; 3 May 1961; Coll: M. A. Carriker.
Sayornis phoebe (Latham)	YPM (no number); USA, Connecticut; Jul 1960; Coll: D. H. Parsons.
Sayornis phoebe (Latham) ad ♂	YPM (field no.) J-766; USA, Connecticut; 28 Aug 1963; Coll: P. L. Ames.
Sayornis phoebe (Latham) imm ♀	YPM (field no.) J-767; USA, Connecticut; 28 Aug 1963; Coll: P. L. Ames.
Sayornis nigricans (Swainson)	USNM 85224; USA, California; 1881; Coll: L. Belding.
Sayornis saya (Bonaparte)	YPM 283; USA, Colorado; 18 Jul 1953; Coll: D. H. Parsons.
Colonia colonus (Vieillot)	AMNH (no number); Panamá; 1924; Coll: C. M. Breder.
Colonia colonus (Vieillot)	AMNH (no number); Panamá; 23 Aug 1923; Coll: unknown.
Colonia colonus (Vieillot)	YPM 2634; Argentina, Misiones; 19 Jan 1961; Coll: P. S. Humphrey.
Gubernetes yetapa (Vieillot)	YPM 2655; Argentina, Corrientes; 19 May 1961; Coll: P. S. Humphrey.
Gubernetes yetapa (Vieillot)	YPM 2654; Argentina, Corrientes; 10 May 1961; Coll: P. S. Humphrey.
Yetapa risora (Vieillot)	USNM 227318; Argentina, Formosa; 18 Aug 1920; Coll: A. Wetmore.
Knipolegus nigerrimus (Vieillot)	AMNH (no number); Brazil; no other data.
Knipolegus cyanirostris (Vieillot)	YPM 2680; Argentina, Misiones; 7 Jul 1961; Coll: P. S. Humphrey.
Knipolegus cyanirostris (Vieillot)	YPM 2681; Argentina, Misiones; 11 Jul 1961; Coll: P. S. Humphrey.
Knipolegus cyanirostris (Vieillot)	YPM 2678; Argentina, Misiones; 8 Jun 1961; Coll: P. S. Humphrey.
Phaeotriccus hudsoni (Sclater)	USNM 227585; Argentina, Victoria; 29 Dec 1920; Coll: A. Wetmore.
Entotriccus striaticeps (Lafr. and D'Orb.)	USNM 227313; Argentina; 13 Aug 1920; Coll: A Wetmore.
Lichenops perspicillata (Gmelin)	YPM 2668; Argentina, Buenos Aires; 24 Oct 1960; Coll: P. S. Humphrey.
Muscipipra vetula (Lichtenstein)	AMNH (no number); Brazil, Paraná; 30 Mar 1030; Coll: E. Kaempfer.
Fluvicola climazura (Vieillot)	AMNH (field no.) 3048; Brazil, Piauí; 8 Jun 1926; Coll: E. Kaempfer.
Arundinicola leucocephala (Linnaeus)	USNM 321638; no data.
Pyrocephalus rubinus (Boddaert) ♂	YPM 2177; Mexico, Campeche; 9 Apr 1962; Coll: E. C. Migdalski.
Pyrocephalus rubinus (Boddaert)	YPM 2176; Mexico, Campeche; 9 Apr 1962; Coll: E. C. Migdalski.
Pyrocephalus rubinus (Boddaert) ♂	YPM 804; Colombia, Magdalena; 27 Jan 1961; Coll: M. A. Carriker, Jr.
Pyrocephalus rubinus (Boddaert) ♀	YPM 2768; Argentina, Misiones; 17 Jun 1961; Coll: P. S. Humphrey.
Pyrocephalus rubinus (Boddaert)	YPM 2766; Argentina, Entre Rios; 1 Apr 1961; Coll: P. S. Humphrey.

Muscigralla brevicauda Lafr. and D'Orb.	AMNH (no number); Peru, Puna Is.; 11 Jul 1932; Coll: unknown.
Satrapa icterophrys (Vieillot)	YPM 2770; Argentina, Entre Rios; 29 Mar 1961; Coll: P. S. Humphrey.
Satrapa icterophrys (Vieillot)	AMNH (no number); Brazil, Rio Grande do Sul; 15 Oct 1928; Coll: E. Kaempfer.
Machetornis rixosa (Vieillot)	YPM 2705; Argentina, Entre Rios; 29 Mar 1961; Coll: P. S. Humphrey.
Machetornis rixosa (Vieillot)	YPM 2709; Argentina, Entre Rios; 30 Apr 1961; Coll: P. S. Humphrey.
Machetornis rixosa (Vieillot)	AMNH (no number); "Brazil or Paraguay;" no other data.

SUBFAMILY TYRANNINAE

Muscivora tyrannus (Linnaeus)	AMNH (no number); Brazil, Paraná; 8 Mar 1962; Coll: E. Kaempfer.
Tyrannus tyrannus (Linnaeus) ♂	YPM 706; USA, Connecticut; 24 May 1961; Coll: D. H. Parsons.
Tyrannus tyrannus (Linnaeus) ♂	YPM (field no.) J-761; USA, Connecticut; date unknown; Coll: D. H. Parsons.
Tyrannus tyrannus (Linnaeus) ♂	YPM (no number); USA, Connecticut; 27 May 1961; Coll: D. H. Parsons.
Tyrannus albogularis Burmeister	YPM 1788; Surinam; 23 Nov 1961; Coll: R. Freund.
Tyrannus melancholicus Vieillot	YPM 1797; Surinam; 25 Nov 1961; Coll: R. Freund.
Tyrannus dominicensis (Gmelin)	YPM 3914; USA, Florida; 12 May 1962; Coll: A. Pflueger.
Empidonomus aurantioatrocristatus (Lafr. and D'Orb.)	YPM 2652; Argentina, Rio Negro; 12 Feb 1961; Coll: P. S. Humphrey.
Legatus leucophaius (Vieillot) ♀	YPM 2136; Mexico, Oaxaca; 22 Mar 1962; Coll: W. J. Schaldach, Jr.
Sirystes sibilator (Vieillot)	YPM 2790; Argentina, Misiones; 11 Jun 1961; Coll: P. S. Humphrey.
Sirystes sibilator (Vieillot)	YPM 2791; Argentina, Misiones; 16 Jun 1961; Coll: P. S. Humphrey.
Myiodynastes luteiventris Sclater	YPM 1048; Colombia, Santander; 29 Apr 1961; Coll: M. A. Carriker, Jr.
Myiodynastes luteiventris Sclater	YPM 1047; Colombia, Santander; 14 Mar 1961; Coll: M. A. Carriker, Jr.
Myiodynastes luteiventris Sclater	WGG 879; USA, Arizona; date unknown; Coll: W. G. George.
Myiodynastes bairdii Gambel	New York Zoological Society; 22 Dec 1962; Col: P. L. Ames.
Megarhynchus pitangua (Linnaeus)	YPM 1550; Mexico, Santa Ana; 7 Jun 1957; Coll: A. Starrett.
Conopias trivirgata (Wied)	YPM 2683; Argentina, Misiones; 11 Jun 1961; Coll: P. S. Humphrey.
Myiozetetes cayanensis (Linnaeus)	YPM 1844; Surinam; 6 Dec 1961; Coll: R. Freund.
Myiozetetes cayanensis (Linnaeus)	YPM 1769; Colombia, Santander; 26 Nov 1961; Coll: M. A. Carriker, Jr.
Myiozetetes cayanensis (Linnaeus)	YPM 2024; Colombia, Magdalena; 22 Feb 1962; Coll: M. A. Carriker, Jr.
Myiozetetes similis (Spix)	YPM 1543; Mexico, Vera Cruz; 12 Jul 1961; Coll: A. R. Phillips.
Myiozetetes similis (Spix)	YPM 2174; Mexico, Campeche; 9 Apr 1962; Coll: M. A. Carriker, Jr.
Myiozetetes similis (Spix)	YPM 1021; Colombia, Magdalena; 24 May 1961; Coll: M. A. Carriker, Jr.

Myiozetetes granadensis Lawrence	AMNH (field no.) 783; Nicaragua; 1917; Coll: W. deW. Miller.
Tyrannopsis sulphurea (Spix)	YPM 5146; New York Zool. Soc.; Feb 1964; Coll: J. Bell.
Pitangus sulphuratus (Linnaeus)	YPM 1533; Mexico, Vera Cruz; 26 Jul 1961; Coll: R. W. Dickerman.
Pitangus sulphuratus (Linnaeus)	AMNH (field no.) 1135; Nicaragua; 1917; Coll: W. deW. Miller.
Pitangus lictor Lichtenstein	YPM 1102; Colombia, Magdalena; 13 Apr 1961; Coll: M. A. Carriker, Jr.
Tolmarchus caudifasciatus (D'Orbigny)	USNM 291915; Cuba; 28 Jul 1928; Coll: P. Bartsch.

SUBFAMILY MYIARCHINAE.

Myiarchus crinitus (Linnaeus)	YPM (no number); USA, Connecticut; 27 May 1960; Coll: D. H. Parsons.
Myiarchus crinitus (Linnaeus)	YPM 759; USA, Connecticut; 5 Mar 1961; Coll: P. L. Ames.
Myiarchus crinitus (Linnaeus)	YPM 1122; USA, Connecticut; 19 May 1961; Coll: G. A. Clark, Jr.
Myiarchus brachyurus Ridgway	AMNH (no number); Nicaragua; 13 Jun 1917; Coll: W. deW. Miller.
Myiarchus tyrannulus (Müller)	YPM 2047; Colombia, Magdalena; 19 Apr 1962; Coll: M. A. Carriker, Jr.
Myiarchus ferox (Gmelin)	YPM 1868; Surinam; 10 Dec 1961; Coll: R. Freund.
Myiarchus tuberculifer (Lafr. and D'Orb.)	YPM 1040; Colombia, Santander; 10 Mar 1961; Coll: M. A. Carriker, Jr.
Myiarchus tuberculifer (Lafr. and D'Orb.)	YPM 1889; Surinam; 11 Dec 1961; Coll: R. Freund
Nesotriccus ridgwayi Townsend	MVZ 3536; Cocos Island, 3 Oct 1965; Coll: R. W. Conard.
Eribates magnirostris (Gould)	USNM 20541; Galapagos Arch., Charles Is.; 8 Apr 1888; Coll: unknown.
Eribates magnirostris (Gould)	USNM 223306; Galapagos Arch., Indefatigable Is.; 12 Apr 1888; Coll: unknown.
Nuttallornis mesoleucus (Lichtenstein)	USNM 226305; USA, Arizona; 14 Jul 1918; Coll: A. Wetmore.
Myiochanes virens (Linnaeus)	YPM (no number); USA, Connecticut; date unknown; Coll: D. H. Parsons.
Myiochanes virens (Linnaeus)	YPM 4301; USA, Connecticut; 24 Sep 1963; Coll: P. L. Ames.
Myiochanes cinereus (Spix)	YPM 2641; Argentina, Misiones; 2 Jul 1961; Coll: P. S. Humphrey.
Blacicus carribaeus (D'Orbigny)	AMNH (no number); Dominican Rep.; 3 Sep 1922; Coll: R. C. Noble.
Empidonax flaviventris (Baird) ♀	YPM (no number); USA, Connecticut; 16 Sep 1961; Coll: D. H. Parsons.
Empidonax minimus (Baird)	YPM 700; USA, Connecticut; 23 May 1961; Coll: D. H. Parsons.
Empidonax minimus (Baird)	YPM 705; USA, Connecticut; 24 May 1961; Coll: P. L. Ames.
Empidonax minimus (Baird) ♂	YPM 4198; USA, Connecticut; 24 Sep 1963; Coll: P. L. Ames.
Empidonax difficilis Baird	YPM 1272; USA, California; 15 Aug 1961; Coll: P. L. Ames.
Empidonax albigularis Scl. and Salv. ♂	YPM 1543; Mexico, Mexico; date unknown; Coll: A. R. Phillips.
Empidonax oberholseri A. R. Phillips ♂	YPM 1544; Mexico, Mexico; 10 Nov 1961; Coll: R. W. Dickerman.

Aechmolophus mexicanus Zimmer ♂	Received from A. R. Phillips; Mexico, Morelos; 19 Jun 1961 1961; Coll: J. S. Rowley; Skin at Univ. Minn. Mus. Zool.
Cnemotriccus poecilurus (Sclater)	AMNH (field no.) 592; Peru; 1915; Coll: E. Heller.
Mitrephanes phaeocercus (Sclater)	MVZ (no number); Mexico, Nayarit; 28 Dec 1960; Coll: R. Stallcup.
Terenotriccus erythrurus (Cabanis)	AMNH (field no.) 867; no data.
Aphanotriccus capitalis (Salvin)	AMNH (field no.) 850; Costa Rica; 1917; Coll: W. deW. Miller.
Myiobius sulphureipygius (Sclater)	WGG 856; USA, Arizona; date unknown; Coll: W. G. George.
Myiobius atricaudatus Lawrence	USNM 343906; Panama; 20 Apr 1937; Coll: Miller and Wheeler.
Pyrrhomyias cinnamomeus (Lafr. and D'Orb.)	YPM 2057; Colombia, Magdalena; 4 Jan 1962; Coll: M. A. Carriker, Jr.
Myiophobus fasciatus (Müller)	YPM 1758; Colombia, Santander; 20 Nov 1961; Coll: M. A. Carriker, Jr.
Onychorhynchus coronatus (Müller) ♂	USNM 195241; Brazil; Jan 1963; Coll: P. S. Humphrey.
Onychorhynchus coronatus (Müller) ♀	USNM 195261; Brazil; Jan 1963; Coll: P. S. Humphrey.

SUBFAMILY PLATYRINCHINAE.

Platyrinchus mystaceus Vieillot	YPM 2758; Argentina, Misiones; 22 Jun 1961; Coll: P. S. Humphrey.
Platyrinchus cancrominus Sclater and Salvin	AMNH (no number); Nicaragua; 13 May 1917; Coll: W. deW. Miller.
Tolmomyias sulphurescens (Spix)	YPM (field no.) C-244; Argentina, Misiones; 19 Jun 1961; Coll: P. S. Humphrey.
Tolmomyias sulphurescens (Spix)	YPM (field no.) C-535; Argentina, Misiones; 3 Jul 1961; Coll: P. S. Humphrey.
Tolmomyias megacephalus (Swainson)	YPM 2769; Argentina, Misiones; 22 Jun 1961; Coll: P. S. Humphrey.
Rhynchocyclus olivaceus (Temminck)	YPM 1095; Colombia, Magdalena; 10 Apr 1961; Coll: M. A. Carriker, Jr.
Rhynchocyclus brevirostris (Cabanis)	YPM 2138; Mexico, Oaxaca; 26 Mar 1961; Coll: W. J. Schaldach, Jr.

SUBFAMILY EUSCARTHMINAE.

Todirostrum cinereum (Linnaeus)	YPM 1538; Mexico, Vera Cruz; 25 Aug 1961; Coll: A. R. Phillips.
Todirostrum sylvia (Desmarest)	YPM 1070; Colombia, Magdalena; 8 Apr 1961; Coll: M. A. Carriker, Jr.
Todirostrum sylvia (Desmarest)	YPM 1763; Colombia, Santander; 21 Nov 1961; Coll: M. A. Carriker, Jr.
Todirostrum plumbeiceps Lafresnaye	YPM 2803; Argentina, Misiones; 13 Jun 1961; Coll: P. S. Humphrey.
Oncostoma cinereigulare (Sclater)	AMNH (field no.) 849; Nicaragua; 1917; Coll: W. deW. Miller.
Euscarthmornis margaritaceiventer (Lafr. and D'Orb.)	USNM 227227; Argentina, Chaco; 9 Jul 1920; Coll: A. Wetmore.
Lophotriccus pileatus (Tschudi) ♀	USNM (no number); Panama; 3 Mar 1951; Coll: A. Wetmore.
Lophotriccus pileatus (Tschudi) ♀	USNM 428193; Panama; 3 Mar 1951; Coll: A. Wetmore.
Colopteryx galeatus (Boddaert)	YPM 1879; Surinam; 10 Dec 1961; Coll: R. Freund.

Myiornis auricularis (Vieillot)	YPM 2725; Argentina, Misiones; 17 Jun 1961; Coll: P. S. Humphrey.
Myiornis auricularis (Vieillot)	YPM 2727; Argentina, Misiones; 21 Jun 1961; Coll: P. S. Humphrey.
Hemitriccus diops (Temminck)	YPM 2662; Argentina, Misiones; 29 Jul 1961; Coll: P. S. Humphrey.
Pogonotriccus eximius (Temminck)	YPM 2759; Argentina, Misiones; 12 Jun 1961; Coll: P. S. Humphrey.
Pogonotriccus eximius (Temminck)	YPM 2762; Argentina, Misiones; 17 Jun 1961; Coll: P. S. Humphrey.
Leptotriccus sylviolus Cab. and Heine	YPM 2694; Argentina, Misiones; 10 Jul 1961; Coll: P. S. Humphrey.
Leptotriccus sylviolus Cab. and Heine	YPM 2693; Argentina, Misiones; 6 Jul 1961; Coll: P. S. Humphrey.
Phylloscartes ventralis (Temminck)	YPM 2753; Argentina, Misiones; 14 Jun 1961; Coll: P. S. Humphrey.
Capsiempis flaveola (Lichtenstein)	AMNH (no number); Nicaragua; 1913; Coll: W. deW. Miller.
Euscarthmus melorhyphus Wied	USNM 227325; Argentina; 23 July 1920; Coll: A. Wetmore.
Corythopis delalandi (Lesson)	YPM 2559; Argentina, Misiones; 30 Jun 1961; Coll: P. S. Humphrey.
Corythopis delalandi (Lesson)	YPM 2611; Argentina, Misiones; 23 Jun 1961; Coll: P. S. Humphrey.
Corythopis delalandi (Lesson)	YPM 2558; Argentina, Misiones; 22 Jun 1961; Coll: P. S. Humphrey.
Corythopis torquata Tschudi ♂	USNM (field no.) 198127; Brazil, Pará; 3 Aug 1964; Coll: P. S. Humphrey.
Corythopis torquata Tschudi ♂	USNM (field no.) 198562; Brazil, Pará; 21 Aug 1964; Coll: P. S. Humphrey.
Pseudocolopteryx sclateri (Oustalet)	USNM 227219; Argentina, Chaco; 27 Jul 1920; Coll: A. Wetmore.
Pseudocolopteryx flaviventris (Lafr. and D'Orb.)	USNM 227207; Argentina, Chaco: 22 Jul 1920; Coll: A. Wetmore.
Habrura pectoralis (Vieillot)	USNM 227218; Paraguay; 3 Sep 1920; Coll: A. Wetmore.
Habrura pectoralis (Vieillot)	YPM 2659; Argentina, Misiones; 21 Jul 1961; Coll: P. S. Humphrey.

SUBFAMILY SERPOPHAGINAE.

Tachuris rubigastra (Vieillot) ♂	YPM 3; Chile; 1958; Coll: L. E. Peña.
Tachuris rubigastra (Vieillot) ♀	YPM 4; Chile; 1958; Coll: L. E. Peña.
Tachuris rubigastra (Vieillot) ♂	YPM 2796; Argentina, Buenos Aires; 4 Aug 1961; Coll: P. S. Humphrey.
Tachuris rubigastra (Vieillot) ♀	YPM 2799; Argentina, Buenos Aires; 19 Aug 1961; Coll. P. S. Humphrey.
Spizitornis parulus (Kittlitz)	YPM 34; Chile; 1958; Coll: L. E. Peña.
Stigmatura budytoides (Lafr. and D'Orb.)	YPM 2783; Argentina, Rio Negro; 12 Feb 1961; Coll: P. S. Humphrey.
Serpophaga subcristata (Vieillot)	YPM 2777; Argentina; Garruchos; 11 May 1961; Coll: P. S. Humphrey.
Inezia subflava (Scl. and Salv.)	CM 71; Venezuela, Guarcia; 10 Sep 1927; Coll: E. G. Holt.
Mecocerculus leucophyrs (Lafr. and D'Orb.)	YPM 970; Colombia, Santander; 3 May 1961; Coll: M. A. Carriker, Jr.
Mecocerculus leucophrys (Lafr. and D'Orb.)	YPM 972; Colombia, Santander; 3 May 1961; Coll: M. A. Carriker, Jr.

Colorhamphus parvirostris (Darwin)	USNM 227983; Chile, Concón; 27 Apr 1927; Coll: A. Wetmore.

SUBFAMILY ELAENIINAE.

Elaenia flavogaster (Thunberg)	YPM 2022; Colombia, Magdalena; 22 Feb 1962; Coll: M. A. Carriker, Jr.
Elaenia martinica (Linnaeus)	YPM 4035; Brit. West Indies, Antigua Is., 25 Mar 1963; Coll: Mrs. F. Olsen.
Elaenia albiceps (Lafr. and D'Orb.)	YPM 2641; Argentina, Tierra del Fuego; 28 Nov 1960; Coll: P. S. Humphrey.
Elaenia chiriquensis (Lawrence)	YPM 2021; Colombia, Santander; 22 Feb 1962; Coll: M. A. Carriker, Jr.
Elaenia chiriquensis (Lawrence)	YPM 1110; Colombia, Santander; 29 Apr 1961; Coll: M. A. Carriker, Jr.
Elaenia chiriquensis (Lawrence)	YPM 1111; Colombia, Santander; 29 Apr 1961; Coll: M. A. Carriker, Jr.
Elaenia obscura (Lafr. and D'Orb.)	YPM 1732; Colombia, Santander; 12 Oct 1961; Coll: M. A. Carriker, Jr.
Elaenia fallax Sclater ♂	YPM 197; Haiti; 5 Mar 1959; Coll: P. S. Humphrey.
Elaenia fallax Sclater ♀	YPM 196; Haiti; 5 Mar 1959; Coll: P. S. Humphrey.
Elaenia gaimardi (D'Orbigny)	YPM 1895; Surinam; 10 Dec 1961; Coll: R. Freund.
Elaenia viridicata (Vieillot)	AMNH (field no.) 1170; Nicaragua; 1913; Coll: W. deW. Miller.
Elaenia caniceps (Swainson)	YPM 2721; Argentina, Misiones; 2 Jul 1961; Coll: P. S. Humphrey.
Suiriri suiriri (Vieillot)	YPM 2788; Argentina, Entre Rios; 21 Apr 1961; Coll: P. S. Humphrey.
Suiriri affinis (Burmeister)	AMNH (no number); Brazil; 23 Jan 1926; Coll: E. Kaempfer.
Sublegatus modestus (Wied)	AMNH (no number); Brazil; 1915; Coll: E. Kaempfer.
Phaeomyias murina (Spix)	YPM 2038; Colombia, Magdalena; 17 Apr 1962; Coll: M. A. Carriker, Jr.
Phaeomyias murina (Spix)	YPM 2046; Colombia, Magdalena; 18 Apr 1962; Coll: M. A. Carriker, Jr.
Camptostoma obsoletum (Temminck)	YPM 2617; Argentina, Misiones; 7 Jun 1961; Coll: P. S. Humphrey.
Camptostoma imberbe Sclater	WGG 845; USA, Arizona; date unknown; Coll: W. G. George.
Tyranniscus chrysops (Sclater)	YPM 922; Colombia, Santander; 10 Mar 1922; Coll: M. A. Carriker, Jr.
Tyranniscus chrysops (Sclater)	YPM 2010; Colombia, Santander; 27 Jan 1962; Coll: M. A. Carriker, Jr.
Tyranniscus nigrocapillus (Lafresnaye)	YPM 2056; Colombia, Santander; 4 Jan 1962; Coll: M. A. Carriker, Jr.
Phyllomyias fasciatus (Thunberg)	USNM 227227; Argentina, Chaco; 27 Jul 1920; Coll: A. Wetmore.
Tyrannulus elatus (Latham)	YPM 1764; Colombia, Santander; 21 Nov 1961; Coll: M. A. Carriker, Jr.
Microtriccus semiflavus (Scl. and Salv.)	YPM 2141; Mexico, Oaxaca; 25 Mar 1962; Coll: W. J. Schaldach, Jr.
Microtriccus semiflavus (Scl. and Salv.)	YPM 1025; Colombia, Magdalena; 25 May 1961; Coll: M. A. Carriker, Jr.
Leptopogon (species unknown)	AMNH (field no.) 819; Nicaragua; 1913; Coll: W. deW. Miller.
Leptopogon (species unknown)	AMNH (field no.) 820; Nicaragua; 1913; Coll: W. deW. Miller.

Leptopogon (species unknown)	AMNH (field no.) 821; Nicaragua; 1913; Coll: W. deW. Miller.
Mionectes olivaceus Lawrence	USNM 430247; Peru; date unknown; Coll: H. F. Allard.
Pipromorpha oleaginea (Lichtenstein)	AMNH (field no.) 865; Nicaragua; 1913; Coll: W. deW. Miller.
Pipromorpha oleaginea (Lichtenstein)	AMNH (no number); Nicaragua; 1917; Coll: W. deW. Miller.
Pipromorpha oleaginea (Lichtenstein)	YPM 1765; Colombia, Santander; 21 Nov 1961; Coll: M. A. Carriker, Jr.

FAMILY OXYRUNCIDAE. SHARPBILL.

Oxyruncus cristatus (Gmelin)	BM (no number); cage bird; 19 Feb 1936; Coll: A. Ezra.

FAMILY PHYTOTOMIDAE. PLANTCUTTERS.

Phytotoma rare Molina	YPM 2874; Argentina, Chubut; 20 Jan 1961; Coll: P. S. Humphrey.
Phytotoma rare Molina	YPM 5; Chile, Nagué; 16-21 Sep 1958; Coll: L. E. Peña.
Phytotoma rutila Vieillot ♂	YPM 2884; Argentina, Buenos Aires; 24 Oct 1960; Coll: P. S. Humphrey.
Phytotoma rutila Vieillot ♀	YPM 2885; Argentina, Buenos Aires; 24 Oct 1960; Coll: P. S. Humphrey.

FAMILY PITTIDAE. PITTAS.

Pitta reichenowi Madarasz	AMNH (no number); Africa, Congo; 11 Oct 1930; Coll: J. P. Chapin.
Pitta boschi Müller and Schlegel	USNM 290038; Sumatra; 1926; K. C. Heller.
Pitta erythrogaster Temminck	AMNH (no number); New Guinea, New Britain; no other data.
Pitta atricapilla Lesson	AMNH (no number); cage bird; 1929; New York Zool. Soc.

FAMILY PHILEPITTIDAE. ASITIES AND FALSE SUNBIRDS.

Philepitta castanea (P.S. Müller)	AMNH (no number); Madagascar; 1929; Coll: Archbold-Rand Exp.
Neodrepanis corsuscans Sharpe	AMNH (no number); Madagascar; no other data.

FAMILY ACANTHISITTIDAE. NEW ZEALAND WRENS.

Acanthisitta chloris (Sparrman)	BM 1904-8-2; New Zealand; no other data.
Xenicus longipes (Gmelin)	BM 1940-12-8-89; New Zealand; Coll: Lord Rothschild.

Suborder Menurae

FAMILY MENURIDAE. LYREBIRDS.

Menura novaehollandiae Latham, nestling	USNM 321461; Australia, New South Wales; 2 Aug 1931; Coll: K. A. Hindwood.

FAMILY ATRICHORNITHIDAE. SCRUB-BIRDS.

Atrichornis clamosus (Gould)	Nat. Mus. Victoria, R-11354; Albany, Western Australia; 25 Jan 1889; Coll: W. Webb.

APPENDIX B

SPECIES OF THE SUBORDER PASSERES EXAMINED

Listed below are the 534 species of oscines examined in this study. Most of the specimens were obtained from the same sources as the suboscines listed in Appendix A; a few were obtained from the Museum of Zoology, University of Michigan, Ann Arbor.

The order of families and family limits are those laid down by Wetmore (1960). Within each family the order and nomenclature of species follow the most recent revision, except as noted. For most families, the reference is the *Check-list of Birds of the World* (Mayr and Greenway, 1960, 1962; Mayr and Paynter, 1964; Paynter, 1967, 1968) or the *Catalogue of the Birds of the Americas* (Hellmayr, 1934-38). When neither of these sources has fully covered a family, I have compiled the list from the most recent regional works and have not cited them individually.

An exception to the above is the assemblage of New World nectar feeders sometimes grouped as the family Coerebidae. The compilers of the *Check-list of Birds of the World* have followed Beecher (1951) in dividing these birds between the Parulidae and Thraupidae, but Lowery and Monroe (in the *Check-list*) noted in their treatment of *Coereba* and *Conirostrum* (including *Atelodacnis*) that the former might warrant family status and the latter might belong in the family Emberizidae. Since my purpose in presenting this list is only to inform the reader of the species that I studied, and not to make taxonomic judgments, I am following Hellmayr (1935) for the Coerebidae.

FAMILY ALAUDIDAE. LARKS.

Ref: Peters, *in* Mayr and Greenway, 1960, p. 3–80.

Mirafra angolensis
Mirafra sabota
Melanocorypha yeltoniensis
Calandrella cinerea (4 specimens)
Calandrella rufescens
Galerida cristata (4 specimens)
Galerida modesta
Alauda arvensis
Eremophila alpestris

FAMILY HIRUNDINIDAE. SWALLOWS.

Ref: Peters, *in* Mayr and Greenway, 1960, p. 80–129.

Pseudochelidon eurystomina (4 specimens)
Pseudochelidon sirintarae
Tachycineta bicolor
Tachycineta albvienter
Tachycineta thalassina
Kalochelidon euchrysea
Progne tapera
Progne subis
Notiochelidon cyanoeuca
Stelgidopteryx ruficollis
Riparia paludicola
Riparia riparia (2 specimens)
Ptyonoprogne obsoleta
Hirundo rustica
Hirundo smithii
Petrochelidon pyrrhonota (2 specimens)
Delichon dasypus

FAMILY CAMPEPHAGIDAE. CUCKOO-SHRIKES.

Coracina pectoralis
Coracina azurea
Coracina montana
Lalage maculosa

FAMILY DICRURIDAE. DRONGOS.

Chaetorhynchus papuensis
Dicrurus aldabranus

FAMILY ORIOLIDAE. OLD WORLD ORIOLES.

Oriolus oriolus
Oriolus larvatus

FAMILY CORVIDAE. CROWS AND JAYS.

Platyophus galericulatus
Cyanocitta cristata (3 specimens)
Aphelocoma coerulescens
Cyanocorax affinis
Cyanocorax yncas
Garrulus glandarius (2 specimens)
Perisoreus canadensis
Urocissa erythrorhyncha
Cissa chinensis

FAMILY CRACTICIDAE. AUSTRALIAN MAGPIES.

Cracticus torquatus
Gymnorhina tibicen

FAMILY GRALLINIDAE. MUD-NEST BUILDERS.

Grallina cyanoleuca
Corcorax melanorhamphos

FAMILY PTILONORHYNCHIDAE. BOWERBIRDS.

Sericulus chrysocephalus
Ptilonorhynchus violaceus

FAMILY PARADISEIDAE. BIRDS OF PARADISE.

Manucodia sp.
Seleucidis melanoleuca

FAMILY SITTIDAE. NUTHATCHES.

Sitta europaea (2 specimens)
Sitta pygmaea

Ref: Peters, Mayr and Deignan, *in* Mayr and Greenway, 1960, p. 167–221.

Campephaga phoenicea
Pericrocotus flammeus
Hemipus picatus
Terphrodornis pondicerianus

Ref: Vaurie, *in* Mayr and Greenway, 1962, p. 137–157.

Dicrurus hottentottus (2 specimens)
Dicrurus paradiseus (2 specimens)

Ref: Greenway, *in* Mayr and Greenway, 1962, p. 122–137.

Oriolus traillii
Sphecotheres flaviventris

Ref: Blake and Vaurie, *in* Mayr and Greenway, 1962, p. 204–282.

Cyanopica cyana
Dendrocitta occipitalis
Pica pica (2 specimens)
Nucifraga columbiana
Corvus brachyrhynchos (11 specimens)
Corvus corone
Corvus macrorhynchos
Corvus ruficollis
Corvus corax

Ref: Amadon, *in* Mayr and Greenway, 1962, p. 166–172.

Ref: Mayr, *in* Mayr and Greenway, 1962, p. 159–160.

Ref: Mayr, *in* Mayr and Greenway, 1962, p. 172–181.

Ref: Mayr, *in* Mayr and Greenway, 1962, p. 181–204.

Ref: Greenway, *in* Paynter, 1967, p. 125–149.

Sitta krueperi
Sitta neumayer

Sitta pusilla
Sitta canadensis (2 specimens)
Sitta carolinensis
Sitta frontalis
Neositta chrysoptera (2 specimens)
Daphoenositta miranda

FAMILY PARIDAE. TITMICE.

Ref: Snow, *in* Paynter, 1967, p. 52–124.

Aegothalos concinnus
Auriparus flaviceps
Parus artricapillus
Parus bicolor
Melanochlora sultanea

FAMILY HYPOSITTIDAE. CORAL-BILLED NUTHATCH.

Ref: Greenway, *in* Paynter, 1967, p. 124.

Hypositta corallirostris

FAMILY CERTHIIDAE. CREEPERS.

Ref: Greenway, *in* Paynter, 1967, p. 150–166.

Certhia familiaris (2 specimens)
Rhabdornis mysticalis
Climacteris rufa (3 specimens)

FAMILY CHAMAEIDAE. WRENTIT.

Ref: Hellmayr, 1934.

Chamaea fasciata

FAMILY TIMALIIDAE. BABBLERS.

Ref: Deignan, *in* Mayr and Paynter, 1964, p.228–442.

Orthonyx temminckii
Orthonyx spaldingii (2 specimens)
Psophodes olivaceus
Cinclosoma ajax
Ifrita kowaldi
Pellorneum ruficeps
Trichastoma tickelli
Pomatorhinus erythrogenys
Pomatorhinus ferruginosus
Neomixis tenella
Neomixis viridis
Stachyris pyrrhops
Stachyris nigriceps
Macronus flavicollis
Macronus gularis
Timalia pileata
Turdoides fulvus
Turdoides gymnogenys
Garrulax delesserti
Garrulax mitratus
Garrulax canorus
Leiothrix lutea
Minla cyanouroptera
Minla strigula
Heterophasia capistrata
Yuhina flavicollis
Yuhina gularis
Yuhina nigrimenta
Yuhina zantholeuca
Malia gratia
Oxylabes madagascariensis
Picathartes gymnocephalus

FAMILY PARADOXORNITHIDAE. PARROT-BILLS.

Ref: Delacour, *in* Mayr and Greenway, 1960, p. 430–442.

Panurus biarmicus
Paradoxornis unicolor
Paradoxornis gularis

FAMILY PYCNONOTIDAE. BULBULS.

Ref: Rand and Deignan, *in* Mayr and Greenway, 1960, p. 221–300.

Pycononotus jocosus
Pycnonotus barbatus
Pycnonotus virens
Pycnonotus latirostris
Pycnonotus tephrolaemus
Chlorocichla simplex
Phyllastrephus zosterops
Bleda syndactyla
Nicator chloris
Criniger calurus
Criniger flaveolus
Hypsipetes charlottae

Chlorocichla flavicollis
Phyllastrephus strepitans
Phyllastrephus madagascariensis
Hypsipetes mcclellandii
Hypsipetes virescens
Hypsipetes madagascariensis (2 specimens)

FAMILY CHLOROPSEIDAE. LEAFBIRDS.

Ref: Delacour, *in* Mayr and Greenway, 1960, p. 300–308.

Aegithina lafresnayi
Chloropsis cochinchinensis
Chloropsis hardwicki
Irena puella (2 specimens)

FAMILY CINCLIDAE. DIPPERS.

Ref: Greenway, *in* Mayr and Greenway, 1960, p. 374–379.

Cinclus cinclus
Cinclus mexicanus

FAMILY TROGLODYTIDAE. WRENS.

Ref: Paynter and Vaurie, *in* Mayr and Greenway, 1960, p. 379–440.

Campylorchynchus zonatus (3 specimens)
Cinnycerthia unirufa
Cistothorus palustris
Thryothorus atrogularis
Thryothorus rutilus
Thryothorus pleurostictus
Troglodytes aedon
Microcerculus marginatus (2 specimens)
Cyphorhinus aradus (2 specimens)

FAMILY MIMIDAE. MIMICS.

Ref: Davis and Miller, *in* Mayr and Greenway, 1960, p. 440–458.

Dumatella carolinensis
Melanoptila glabrirostris
Mimus polyglottos
Mimus gilvus
Mimodes graysoni
Oreoscoptes montanus
Toxostoma rufum
Cinclocerthia ruficauda
Donacobius atricapillus

FAMILY TURDIDAE. THRUSHES.

Ref: Ripley, *in* Mayr and Paynter, 1964, p. 13–227.

Brachypteryx montana
Erythropygia leucophrys
Erythropygia barbata
Pogonocichla stellata
Erithacus sharpei
Erithacus gunningi
Erithacus rubecula
Erithacus cyanurus
Phoenicurus phoenicurus
Phoenicurus frontalis
Phoenicurus auroreus
Cinclidium frontale
Sialia sialis
Sialia currucoides
Enicurus scouleri
Enicurus maculatus
Myadestes townsendi
Myadestes genibarbis (2 specimens)
Myadestes unicolor
Stizorhina fraseri
Cercomela familiaris
Saxicola rubetra
Saxicola torquata
Myrmecocichla arnotti (2 specimens)
Oenanthe isabellina
Cossypha natalensis
Cossypha niveicapilla
Cichladusa guttata
Alethe fuelleborni
Alethe montana
Copsychus saularis
Copsychus sechellarum
Copsychus malabaricus
Chaimarrornis leucocephalus
Saxicoloides fulicata
Monticola brevipes
Monticola solitarius
Myiophoneus caeruleus (2 specimens)
Zoothera naevia
Zoothera pinicola
Zoothera dauma
Catharus gracilirostris
Catharus occidentalis
Catharus fuscescens
Catharus minimus
Catharus ustulatus
Catharus guttatus
Hylocichla mustelina
Turdus litsipsirupa
Turdus plumbeus (2 specimens)

Oenanthe oenanthe (2 specimens)
Oenanthe deserti
Oenanthe hispanica
Oenanthe leucopyga
Oenanthe pileata
Turdus leucomelas
Turdus amaurochalinus
Turdus nudigenis
Turdus migratorius (4 specimens)

FAMILY ZELEDONIIDAE. WREN-THRUSH.

Ref: Ripley, *in* Paynter, 1964, p. 18.

Zeledonia coronata.

FAMILY SYLVIIDAE. OLD WORLD WARBLERS.

Ref: Regional works.

Tesia superciliosus
Cettia diphone
Cettia montana
Bradypterus castaneus
Bradypterus cinnamomeus (2 specimens)
Calamonastes fasciolatus
Melocichla mentalis
Cisticola chiniana
Cisticola cherrina
Cisticola brachyptera
Camaroptera brevicauda
Sylvietta brachyura
Prinia gracilis
Prinia atrogularis
Apalis flavida
Orthotomus astrogularis
Orthotomus cephium
Locustella ochotensis
Schoenicola brevirostris
Phragmaticola aëdon
Polioptila caerulea
Polioptila dumicola
Microbates cinereiventris
Rhamphocaenus melanurus
Lamprolia victoriae
Acrocephalus schoenobaenus
Acrocephalus scirpaceus
Acrocephalus caffra
Conopoderas familiaris
Cinclorhamphus cruralis
Hippolais icterinus
Hippolais pallida
Sylvia borin
Sylvia cantilans
Sylvia curruca
Sylvia melanocephala
Sylvia atricapilla
Phylloscopus sibilatrix
Phylloscopus coronatus
Phylloscopus trochilus
Seicercus ruficapilla
Seicercus burkei
Seicercus nouhuysei
Artisornis metopias
Abroscopus schistaceps
Hylia prasina
Malurus gouldi
Stipiturus malachurus
Gerygone flavolateralis
Sericornis magnirostris
Vitia ruficapilla

FAMILY REGULIDAE. KINGLETS.

Ref: Hellmayr, 1932.

Regulus calendula (2 specimens)
Regulus satrapa (2 specimens)

FAMILY MUSCICAPIDAE. OLD WORLD FLYCATCHERS.

Ref: Vaurie, 1953 (Muscicapinae); Paynter, 1967, p. 3–57 (Pachycephalinae); regional works (remainder).

Melaenornis chocolatina
Melaenornis edolioides
Melaenornis pammelaina
Ficedula hypoleuca
Ficedula albicollis
Ficedula monileger
Ficedula cyanomelaena
Niltava macgrigoriae
Niltava sundara
Niltava rubeculoides
Muscicapa striata
Tchitrea corvina
Erythrocercus mccalli
Monarcha alecto
Monarcha barbata
Monarcha axillaris
Monarcha guttula
Myiagra caledonica
Myiagra azureocapilla
Casiempis gayi
Arses telescophthalmus
Chelidorhynx hypoxanthura

Muscicapa sibirica
Muscicapa latirostris
Newtonia brunneicauda
Newtonia archboldi
Culicicapa ceylonensis
Pseudobias wardi
Diaphorophyia castanea
Batis minor
Trochocercus cyanomelas
Erranornis longicauda
Terpsiphone rufiventris
Petroica multicolor
Peneothello sigillata
Pachycephala pectoralis
Pachycephala schlegelii
Clytorhynchus pachycephaloides
Clytorhynchus nigrogularis
Peltops blainvillei
Pitohui dichrous
Rhipidura rufiventris
Rhipidura albolimbata
Rhipidura brachyrhynchus

FAMILY PRUNELLIDAE. ACCENTORS.

Ref: Ripley, *in* Mayr and Paynter, 1964, p. 3–12.

Prunella collaris (2 specimens)
Prunella montanella
Prunella modularis

FAMILY MOTACILLIDAE. WAGTAILS AND PIPITS.

Ref: Vaurie, White, Mayr and Greenway, *in* Mayr and Greenway, 1960, p. 129–167.

Motacilla flava
Motacilla cinerea (2 specimens)
Motacilla flaviventris
Anthus spinoletta

FAMILY BOMBYCILLIDAE. WAXWINGS.

Ref: Greenway, *in* Mayr and Greenway, 1960, p. 369–371.

Bombycilla garrulus
Bombycilla cedrorum

FAMILY PTILOGONATIDAE. SILKY FLYCATCHERS.

Ref: Greenway, *in* Mayr and Greenway, 1960, p. 371–373, 458.

Ptilogonys cinereus
Phainopepla nitens
Phainoptila melanoxantha

FAMILY DULIDAE. PALM CHAT.

Ref: Greenway, *in* Mayr and Greenway, 1960, p. 373–374.

Dulus dominicus (4 specimens)

FAMILY ARTAMIDAE. WOOD SWALLOWS.

Ref: Mayr, *in* Mayr and Greenway, 1962, p. 160–165.

Artamus leucorhynchus
Artamus maximus
Artamus cyanopterus

FAMILY VANGIDAE. VANGA SHRIKES.

Ref: Rand, *in* Mayr and Greenway, 1960, p.365–369.

Calicalicus madagascariensis
Schetba rufa
Vanga curvirostris
Falculea palliata
Leptopterus viridis
Leptopterus chabert
Leptopterus madagascarinus
Euryceros prevostii

FAMILY LANIIDAE. TYPICAL SHRIKES.

Ref: Rand, *in* Mayr and Greenway, 1960, p. 314–365.

Lanioturdus torquatus
Corvinella melanoleuca

Dryoscopus sabini
Tchagra minuta

Laniarius ferrugineus
Laniarius atrococcineus

Lanius cristatus
Lanius schach

Lanius nubicus
Pityriasis gymnocephala

FAMILY PRIONOPIDAE. HELMET SHRIKES.

Ref: Rand, *in* Mayr and Greenway, 1960, p. 309–314.

Eurocephalus rüppelli
Eurocephalus anguitimens
Prionops plumata
Prionops retzii
Prionops scopifrons

FAMILY CYCLARHIDAE. PEPPERSHRIKES.

Ref: Blake, *in* Paynter, 1968, p. 103–108.

Cyclarhis gujanensis

FAMILY VIREOLANIIDAE. SHRIKE-VIREOS.

Ref: Blake, *in* Paynter, 1968, p. 108–110.

Vireolanius pulchellus

FAMILY CALLEIDAE. WATTLEBIRDS.

None examined.

FAMILY STURNIDAE. STARLINGS.

Ref: Amadon, *in* Mayr and Greenway, 1962, p. 75–121.

Aplonis atrifusca
Aplonis tabuensis (2 specimens)
Aplonis opaca
Aplonis metallica
Onychognathus morio
Lamprotornis chloropterus
Lamprotornis acuticaudus
Cinnyricinclus sharpii
Cinnyricinclus leucogaster
Spreo superbus
Cosmopsarus unicolor
Saroglossa aurata
Creatophora cinerea
Sturnus roseus
Sturnus vulgaris (2 specimens)
Sturnus contra (2 specimens)
Sturnus nigricollis
Acridotheres tristis
Acridotheres grandis
Mino dumontii
Sarcops calvus
Gracula religiosa
Scissirostrum dubium
Buphagus erythrorhynchus

FAMILY MELIPHAGIDAE. HONEYEATERS.

Ref: Salomonsen, *in* Paynter, 1967, p. 338-450.

Timeliopsis fulvigula
Lichmera indistincta
Myzomela nigrita
Meliphaga gracilis
Meliphaga fusca
Meliphaga subfrenata
Ptiloprora guisei
Melidectes princeps
Melidectes belfordi
Vosea whitemanensis
Moho braccatus
Acanthorhynchus tenuirostris
Promerops cafer

FAMILY NECTARINIIDAE. SUNBIRDS.

Ref: Rand, *in* Paynter, 1967, p. 208–289.

Anthreptes singalensis
Nectarinia asiatica
Arachnothera longirostra

FAMILY DICAEIDAE. FLOWERPECKERS.

Ref: Salomonsen, *in* Paynter, 1967, p. 166–208.

Melanocharis nigra
Dicaeum celebicum
Dicaeum trochileum
Paramythia montium

FAMILY ZOSTEROPIDAE. WHITE-EYES.

Ref: Mayr and Moreau, *in* Paynter, 1967, p. 289–337.

Zosterops erythropleura
Zosterops lateralis
Zosterops montana
Woodfordia lacertosa
Chlorocharis emiliae
Zosterops senegalensis
Zosterops maderaspatana
Speirops lugubris

FAMILY VIREONIDAE. VIREOS.

Ref: Blake, *in* Paynter, 1968, p. 110–138.

Vireo griseus
Vireo nanus
Vireo olivaceus
Vireo gilvus
Hylophilus ochraceiceps

FAMILY COEREBIDAE. HONEYCREEPERS.

Ref: Hellmayr, 1935, Part 8, p. 218–331.

Coereba flaveola
Atelodacnis speciosa
Dacnis lineata
Euneornis campestris

FAMILY DREPANIDIDAE. HAWAIIAN HONEYCREEPERS.

Ref: Greenway, *in* Paynter, 1968, p. 93–103.

Himantione sanguinea
Vestiaria coccinea
Hemignathus obscurus
Hemignathus wilsoni
Viridonia virens
Psittirostra psittacea
Loxioides cantans

FAMILY PARULIDAE. NEW WORLD WARBLERS.

Ref: Lowery and Monroe, *in* Paynter, 1968, p. 3–82.

Mniotilta varia
Vermivora pinus
Dendroica caerulescens
Dendroica virens
Dendroica palmarum (2 specimens)
Dendroica striata
Dendroica castanea
Setophaga ruticilla
Seiurus aurocapillus
Helmintheros vermivorus
Prothonotaria citrea
Geothlypis agilis
Microligea palustris
Teretistris fornsi
Myioborus ornatus
Peucedramus olivaceus
Xenoligea montana
Granatellus venustus
Granatellus sallaei
Icteria virens

FAMILY PLOCEIDAE (INCLUDING ESTRILDIDAE). WEAVER-FINCHES AND WAXBILLS.

Ref: Moreau and Greenway, *in* Mayr and Greenway, 1962, p. 3–75; Mayr, *in* Paynter, 1968, p. 306–390.

Passer domesticus (8 specimens)
Euplectes orix
Chloebia gouldiae
Padda oryzivora

FAMILY ICTERIDAE. TROUPIALS.

Ref: Blake, *in* Paynter, 1968, p. 138–202.

Cacicus holocericeus
Icterus galbula
Agelaius phoeniceus (2 specimens)
Sturnella magna (3 specimens)
Sturnella neglecta
Quiscalus quiscula
Molothrus ater

FAMILY TERSINIDAE. SWALLOW TANAGER.

Ref: Hellmayr, 1936, part 9, p. 1–6.

Tersina viridis

FAMILY THRAUPIDAE. TANAGERS.

Ref: Hellmayr, 1936, p. 6–446.

Tanagra luteicapilla
Calospiza (= Tangara) cyanicollis
Calospiza (= Tangara) gyrola
Stephanophorus diadematus
Bangsia edwardsi
Thraupis episcopus (= virens)
Thraupis palmarum
Spindalis zena
Ramphocoelus icteronotus
Piranga olivacea (2 specimens)
Habia gutturalis (2 specimens)
Rhodinocichla rosea
Calyptophilus frugivorus
Hemithraupis guira
Nesospingus speculiferus
Schistochlamys melanops

FAMILY FRINGILLIDAE. SPARROWS AND BUNTINGS.

Ref: Hellmayr, 1938, Part 11, 662 p.; Howell and Paynter, *in* Paynter, 1968, p. 207–306.

Saltator albicollis
Gubernatrix cristata
Paroaria coronata
Richmondena cardinalis
Hedymeles ludovicianus
Hedymeles melanocephalus
Passerina cyanea (2 specimens)
Fringilla coelebs
Montifringilla nivalis
Pinaroloxias inornatus
Carduelis chloris
Carduelis pinus
Carduelis carduelis
Acanthis flammea
Carpodacus purpureus
Pinicola enucleator
Loxia curvirostra
Coccothraustes vespertinus
Loxigilla violacea
Sporophila minuta
Volatinia jacarina
Sicalis lebruni
Diuca diuca
Phrygilus patagonicus
Phrygilus gayi
Phrygilus fruticeti
Phrygilus carbonarius
Melanodera melanodera
Coryphospingus cucullatus
Atlapetes albofrenatus
Arremon aurantiirostris
Arremonops conirostris
Piplio erythrophthalmus
Myiospiza humeralis
Passerculus sandwichensis
Ammodramus savannarum
Ammospiza caudacuta
Ammospiza maritima
Chondestes grammacus
Aimophila strigiceps
Amphispiza bilineata
Junco hyemalis
Junco oreganus
Spizella pusilla
Zonotrichia albicollis
Zonotrichia capensis
Passerella iliaca
Melospiza melodia (2 specimens)
Emberizoides herbicola
Poospiza torquata (2 specimens)
Saltricula multicolor
Embernagra platensis
Calcarius lapponicus (4 specimens)
Plectrophenax nivalis
Emberiza melanocephala

INDEX

This index is intended to provide the reader with reference to morphological descriptions and taxonomic discussion only. The pages indicated in Roman type contain morphological descriptions; those in italics contain taxonomic discussion. The two page references (which may be the same) following the generic name locate descriptions of syringeal cartilages and musculature, respectively. If one of these aspects of the syrinx is not described, a dash is provided in order to identify the single page reference.

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PLATES

The following plates represent the majority of syringeal variations encountered in this study. To facilitate comparisons, all syringes are shown at about the same size, instead of to the same scale. The figures therefore represent various magnifications of the actual syringes rounded to the nearest integer. Where great variability exists among the specimens of a species, the specimen number of the individual drawn is indicated in the relevant caption. Where no number is given, either the species is uniform in structure, or only a single individual was examined.

In all the plates the stippled areas represent bone or cartilage, with no attempt to differentiate between various cartilage tissue types. Clear areas within each figure are membranous or, when continuous with muscle (as in *Legatus,* Pl. 8), tendinous.

PLATE 1

Nomenclature

Fig. 1 Configurations of cartilaginous elements.

Fig. 2 Oblique views and sections of the right halves of typical divided A- and B-elements.

Fig. 3 Simplified tracheobronchial junction in ventrilateral view, showing extrinsic syringeal muscles: M. sternotrachealis and M. tracheolateralis.

Fig. 4 Same, showing only M. obliquus ventralis.

Fig. 5 Same, showing M. obliquus lateralis; M. obliquus ventralis cut away.

Fig. 6 Simplified tracheobronchial junction, dorsolateral view, showing M. obliquus dorsalis, internal tympaniform membrane, and internal cartilage.

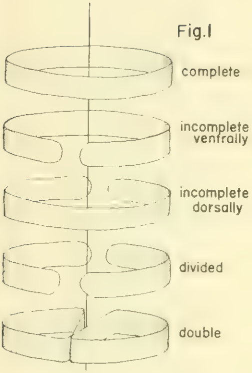


Fig.1
complete
incomplete ventrally
incomplete dorsally
divided
double

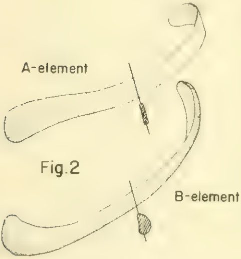


Fig.2
A-element
B-element

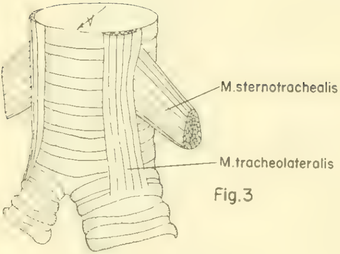


Fig.3
M.sternotrachealis
M.tracheolateralis

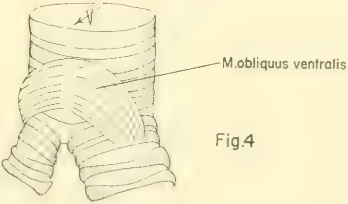


Fig.4
M.obliquus ventralis

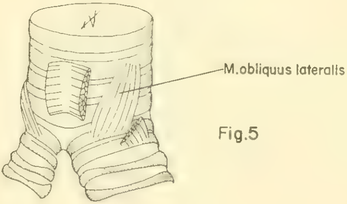


Fig.5
M.obliquus lateralis

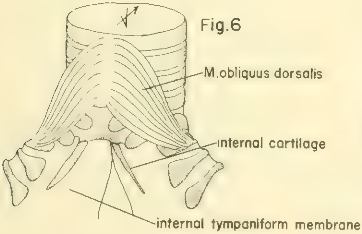


Fig.6
M.obliquus dorsalis
internal cartilage
internal tympaniform membrane

PLATE 2

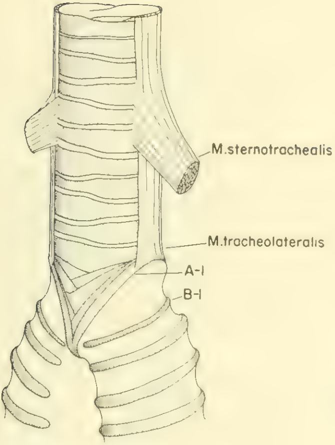
Eurylaimidae

Psarisomus dalhousei, ventrilateral view, ×8.

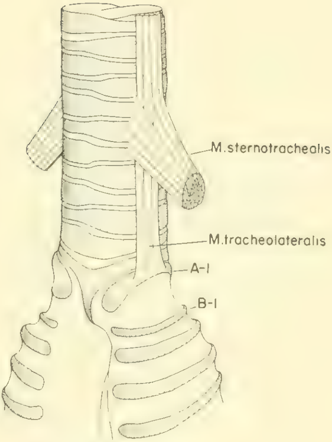
Same, dorsolateral view, ×8.

Calyptomena whiteheadi, ventrilateral view, ×5.

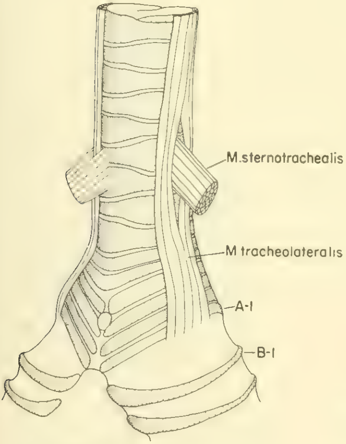
Same, dorsolateral view, ×5.


M.sternotrachealis
M.tracheolateralis
A-1
B-1

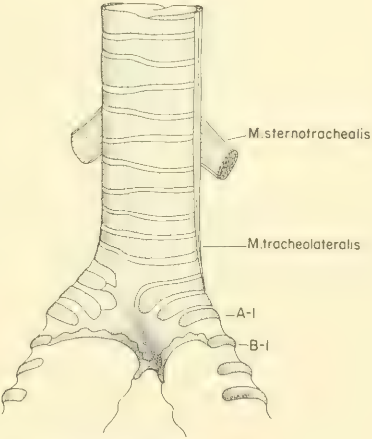
Psarisomus, ventral


M.sternotrachealis
M.tracheolateralis
A-1
B-1

Psarisomus, dorsal


M.sternotrachealis
M tracheolateralis
A-1
B-1

Calyptomena, ventral


M.sternotrachealis
M.tracheolateralis
A-1
B-1

Calyptomena, dorsal

PLATE 3

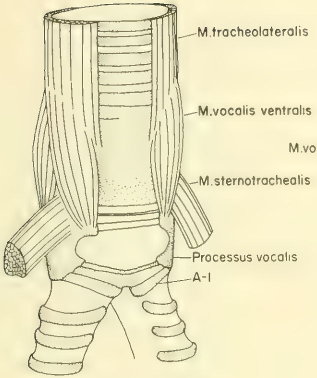
Furnarioidea (I)

Campylorhamphus trochilirostris, (Dendrocolaptidae), ventrilateral view, ×6.

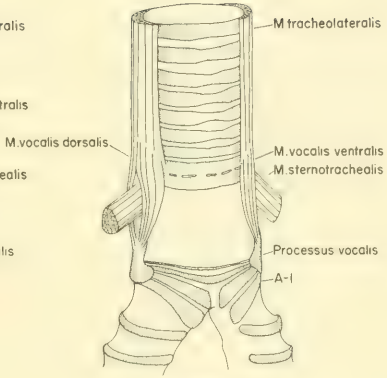
Cinclodes fuscus (Furnariidae), ventrilateral view, ×6.

Taraba major (Formicariidae), ventrilateral view, ×6.

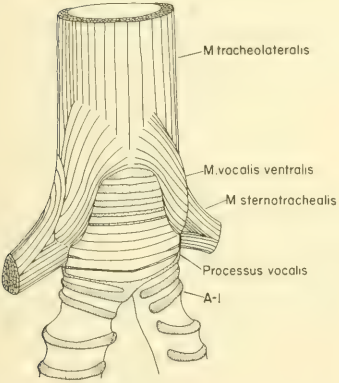
Formicarius analis (Formicariidae), ventrilateral view, ×6.


M.tracheolateralis
M.vocalis ventralis
M.sternotrachealis
Processus vocalis
A-1

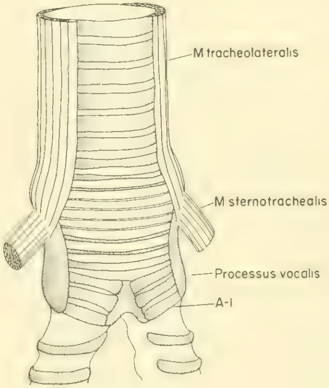
Campylorhamphus


M tracheolateralis
M.vocalis dorsalis
M.vocalis ventralis
M.sternotrachealis
Processus vocalis
A-1

Cinclodes


M tracheolateralis
M.vocalis ventralis
M sternotrachealis
Processus vocalis
A-1

Taraba


M tracheolateralis
M sternotrachealis
Processus vocalis
A-1

Formicarius

PLATE 4

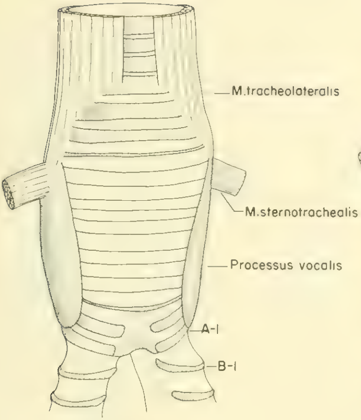
Furnarioidea (II)

Chamaeza brevicauda (Formicariidae), ventrilateral view, ×6.

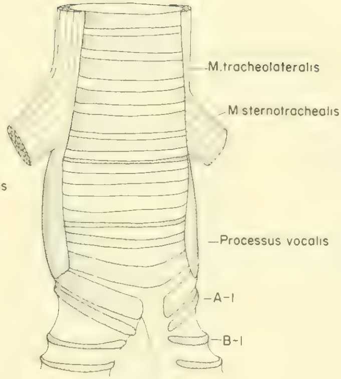
Conopophaga roberti (Formicariidae), ventrilateral view, ×8.

Melanopareia maximilliani (Rhinocryptidae), ventrilateral view, ×6.

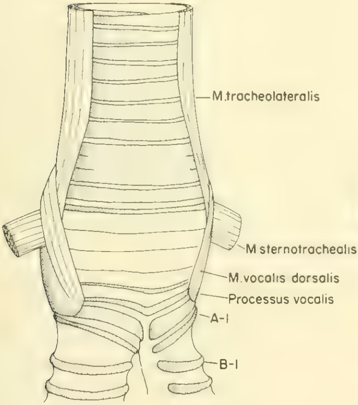
Pteroptochos tarnii (Rhinocryptidae), ventrilateral view, ×5.


M.tracheolateralis
M.sternotrachealis
Processus vocalis
A-I
B-I

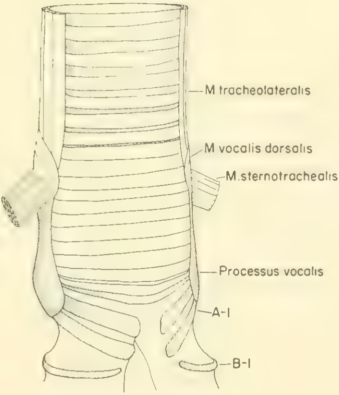
Chamaeza


M.tracheolateralis
M sternotrachealis
Processus vocalis
A-I
B-I

Conopophaga


M.tracheolateralis
M sternotrachealis
M.vocalis dorsalis
Processus vocalis
A-I
B-I

Melanopareia


M tracheolateralis
M vocalis dorsalis
M.sternotrachealis
Processus vocalis
A-I
B-I

Pteroptochos

PLATE 5

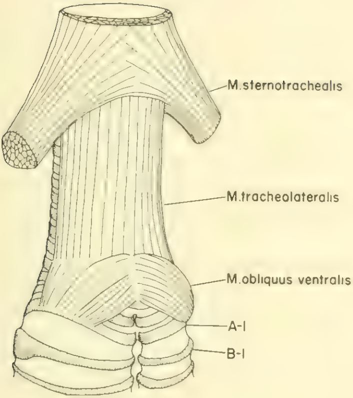
Tyrannidae (I), Ventral

Xolmis irupero, ventrilateral view, ×5.

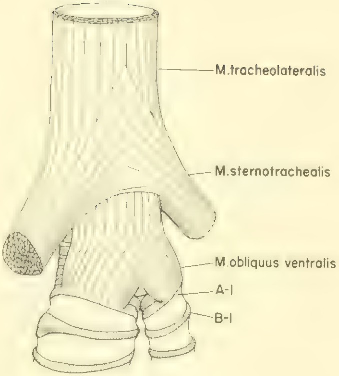
Lessonia rufa, ventrilateral view, ×9.

Sayornis phoebe, ventrilateral view, ×6.

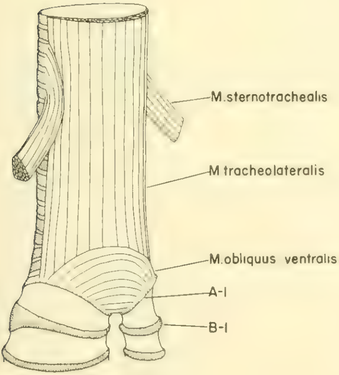
Colonia colonus (YPM 2634), ventrilateral view, ×8.


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-I
B-I

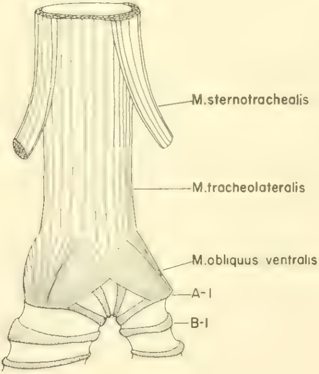
Xolmis


M.tracheolateralis
M.sternotrachealis
M.obliquus ventralis
A-I
B-I

Lessonia


M.sternotrachealis
M tracheolateralis
M.obliquus ventralis
A-I
B-I

Sayornis


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-I
B-I

Colonia

PLATE 6

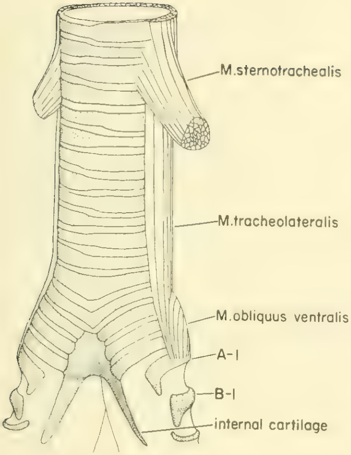
Tyrannidae (I), Dorsal

Xolmis irupero, dorsolateral view, ×5.

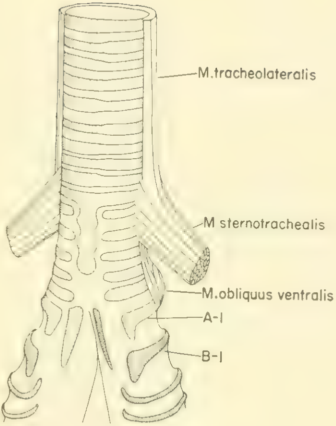
Lessonia rufa, dorsolateral view, ×9.

Sayornis phoebe, dorsolateral view, ×6.

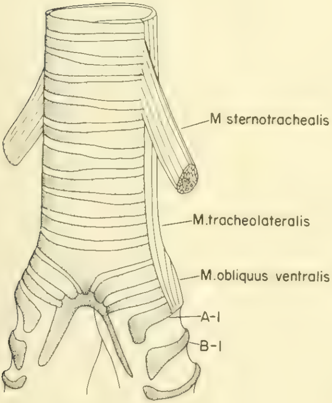
Colonia colonus (YPM 2634), dorsolateral view, ×8.


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-1
B-1
internal cartilage

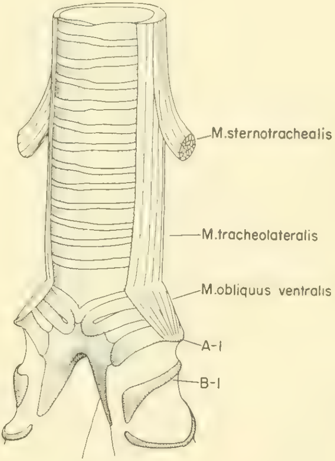
Xolmis


M.tracheolateralis
M sternotrachealis
M.obliquus ventralis
A-1
B-1

Lessonia


M sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-1
B-1

Sayornis


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-1
B-1

Colonia

PLATE 7

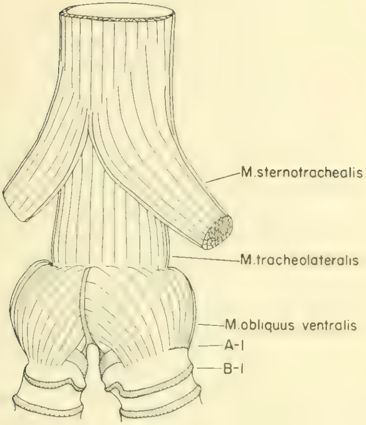
Tyrannidae (II), Ventral

Lichenops perspicillata, ventrilateral view, ×5.

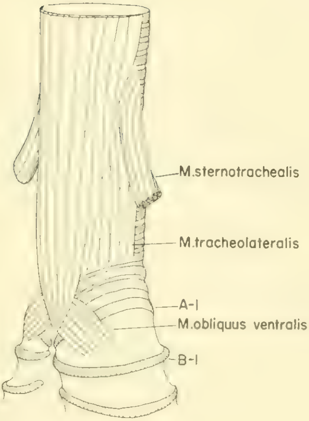
Pyrocephalus rubinus (YPM 2177), ventrilateral view, ×6.

Machetornis rixosa, ventrilateral view, ×5.

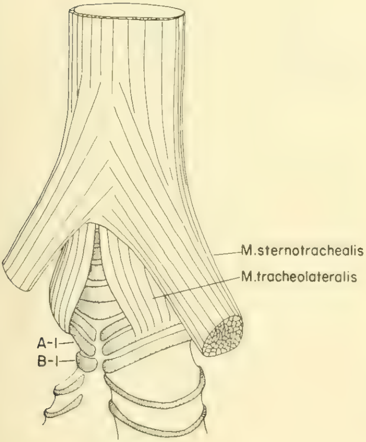
Legatus leucophaius, ventrilateral view, ×6.


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-I
B-I

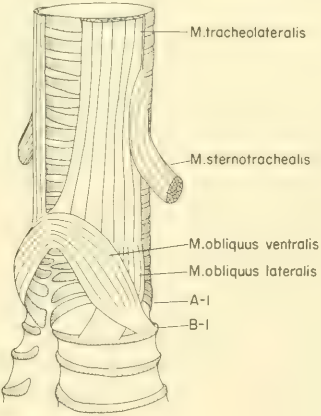
Lichenops


M.sternotrachealis
M.tracheolateralis
A-I
M.obliquus ventralis
B-I

Pyrocephalus


M.sternotrachealis
M.tracheolateralis
A-I
B-I

Machetornis


M.tracheolateralis
M.sternotrachealis
M.obliquus ventralis
M.obliquus lateralis
A-I
B-I

Legatus

PLATE 8

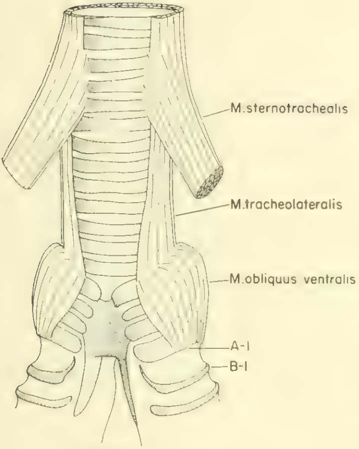
Tyrannidae (II), Dorsal

Lichenops perspicillata, dorsolateral view, ×5.

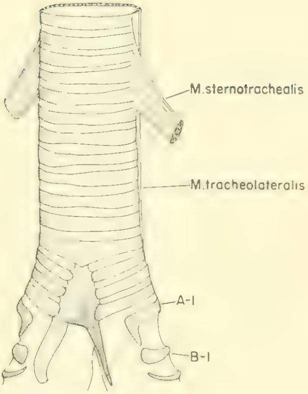
Pyrocephalus rubinus (YPM 2177), dorsolateral view, ×6.

Machetornis rixosa, dorsolateral view, ×5.

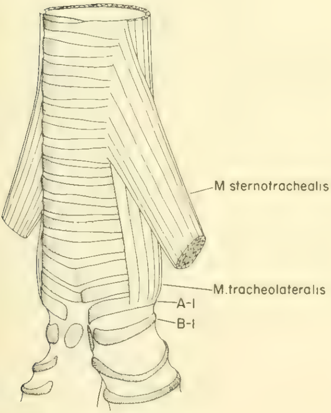
Legatus leucophaius, dorsolateral view, ×5.


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-I
B-I

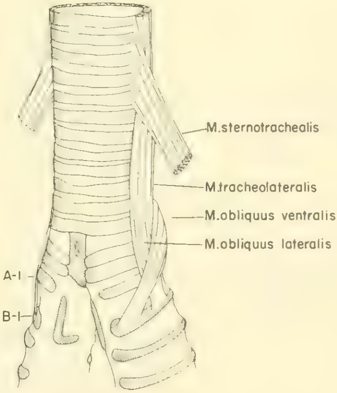
Lichenops


M.sternotrachealis
M.tracheolateralis
A-I
B-I

Pyrocephalus


M sternotrachealis
M.tracheolateralis
A-I
B-I

Machetornis


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
M.obliquus lateralis
A-I
B-I

Legatus

PLATE 9

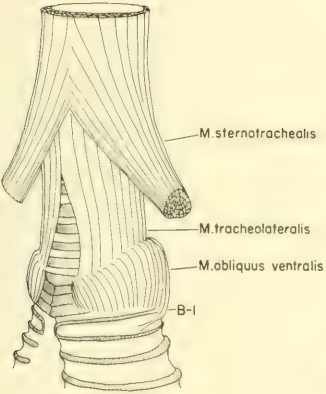
Tyrannidae (III), Ventral

Tyrannus tyrannus (YPM 706), ventrilateral view, ×5.

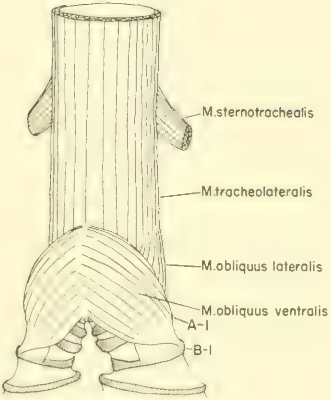
Myiozetetes similis (YPM 1543), ventrilateral view, ×7.

Myiarchus crinitus (YPM 759), ventrilateral view, ×5.

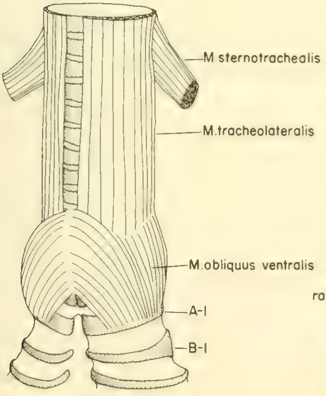
Nuttallornis mesoleucus, ventrilateral view, ×6.


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
B-I

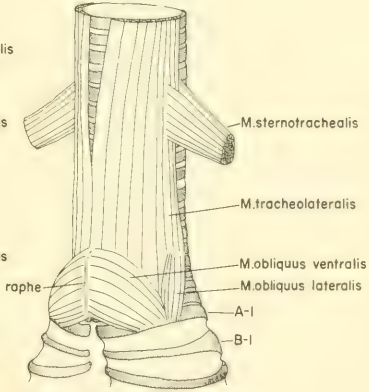
Tyrannus


M.sternotrachealis
M.tracheolateralis
M.obliquus lateralis
M.obliquus ventralis
A-I
B-I

Myiozetetes


M sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-I
B-I

Myiarchus


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
M.obliquus lateralis
raphe
A-I
B-I

Nuttallornis

PLATE 10

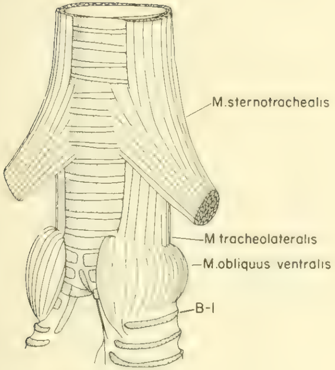
Tyrannidae (III), Dorsal

Tyrannus tyrannus (YPM 706), dorsolateral view, ×5.

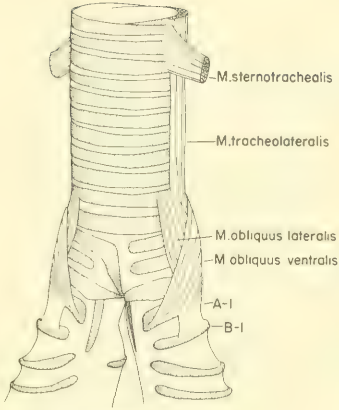
Myiozetetes similis (YPM 1543), dorsolateral view, ×7.

Myiarchus crinitus (YPM 759), dorsolateral view, ×5.

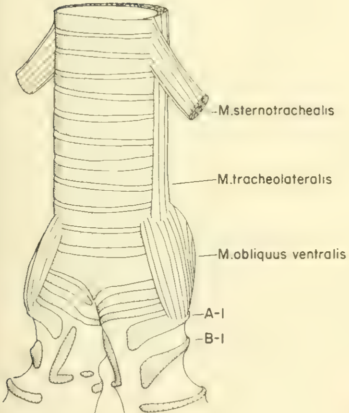
Nuttallornis mesoleucus, dorsolateral view, ×6.


M.sternotrachealis
M tracheolateralis
M.obliquus ventralis
B-I

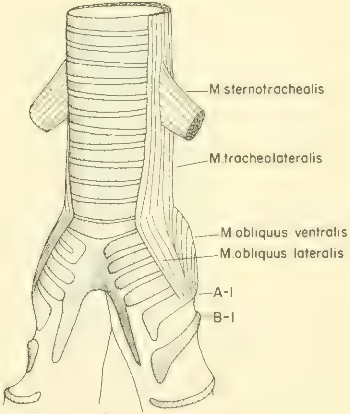
Tyrannus


M.sternotrachealis
M.tracheolateralis
M.obliquus lateralis
M obliquus ventralis
A-I
B-I

Myiozetetes


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-I
B-I

Myiarchus


M sternotrachealis
M.tracheolateralis
M obliquus ventralis
M.obliquus lateralis
A-I
B-I

Nuttallornis

PLATE 11

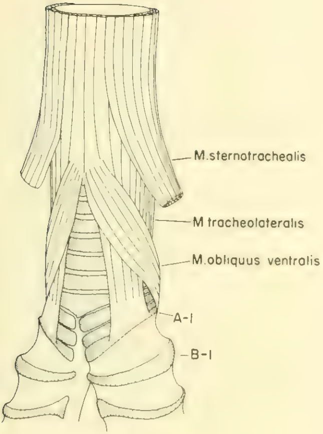
Tyrannidae (IV), Ventral

Platyrinchus mystaceus, ventrilateral view, ×12.

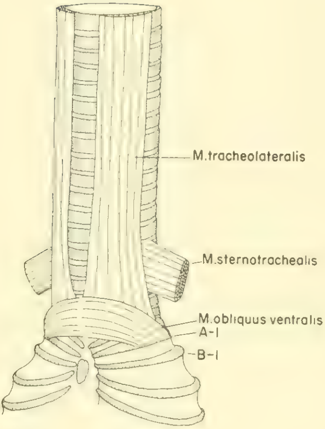
Rhynchocyclus brevirostris, ventrilateral view, ×9.

Todirostrum sylvia (YPM 1763), ventrilateral view, ×12.

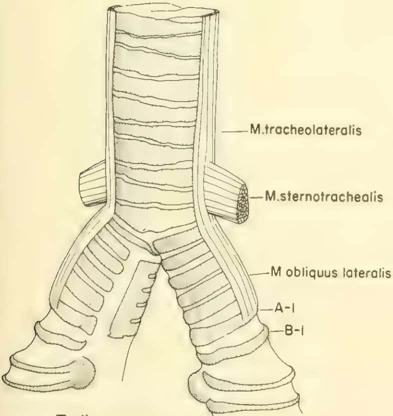
Terenotriccus erythrurus, ventrilateral view, ×12.


M.sternotrachealis
M tracheolateralis
M.obliquus ventralis
A-I
B-I

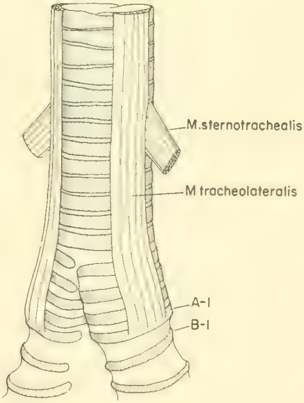
Platyrinchus


M.tracheolateralis
M.sternotrachealis
M.obliquus ventralis
A-I
B-I

Rhynchocyclus


M.tracheolateralis
M.sternotrachealis
M obliquus lateralis
A-I
B-I

Todirostrum


M.sternotrachealis
M tracheolateralis
A-I
B-I

Terenotriccus

PLATE 12

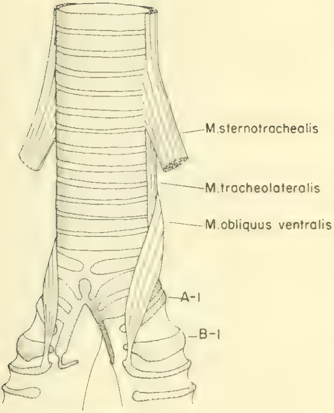
Tyrannidae (IV), Dorsal

Platyrinchus mystaceus, dorsolateral view, × 12.

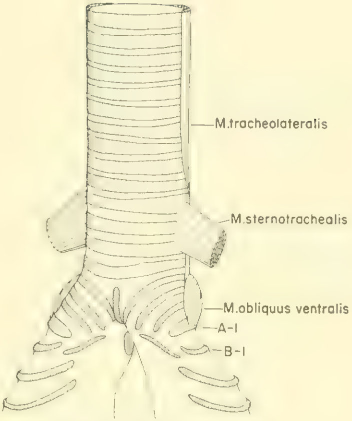
Rhynchocyclus brevirostris, dorsolateral view, × 9.

Todirostrum sylvia (YPM 1763), dorsolateral view, × 12.

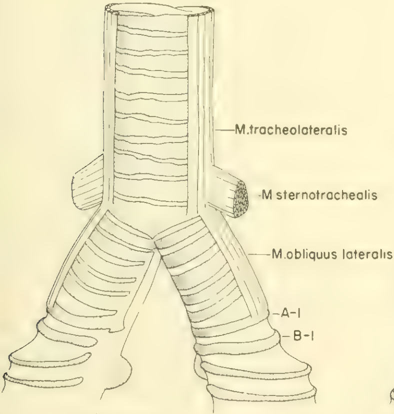
Terenotriccus erythrurus, dorsolateral view, × 12.


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-I
B-I

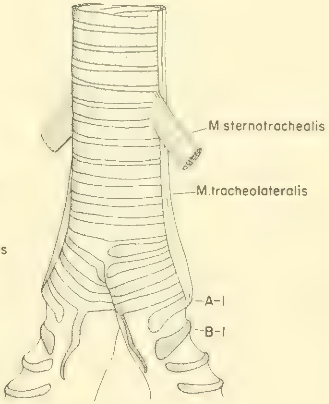
Platyrinchus


M.tracheolateralis
M.sternotrachealis
M.obliquus ventralis
A-I
B-I

Rhynchocyclus


M.tracheolateralis
M sternotrachealis
M.obliquus lateralis
A-I
B-I

Todirostrum


M sternotrachealis
M.tracheolateralis
A-I
B-I

Terenotriccus

PLATE 13

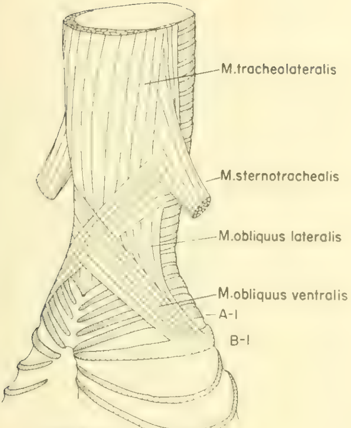
Tyrannidae (V), Ventral

Colopteryx galeata, ventrilateral view, ×12.

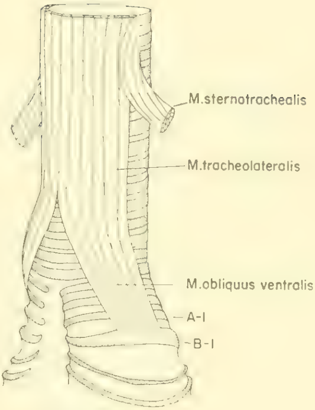
Tachuris rubrigastra, ventrilateral view, ×14.

Elaenia viridicata, ventrilateral view, ×8.

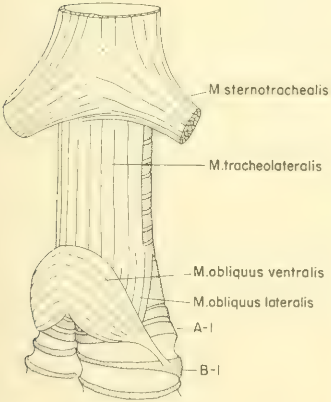
Pipromorpha oleaginea, ventrilateral view, ×9.


M.tracheolateralis
M.sternotrachealis
M.obliquus lateralis
M.obliquus ventralis
A-I
B-I

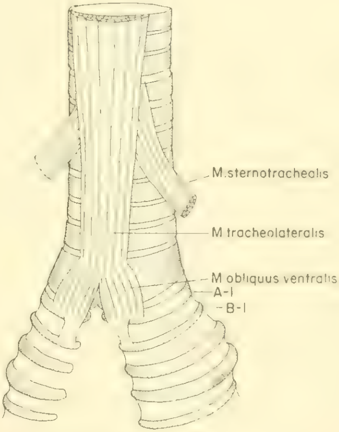
Colopteryx


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
A-I
B-I

Tachuris


M sternotrachealis
M.tracheolateralis
M.obliquus ventralis
M.obliquus lateralis
A-I
B-I

Elaenia


M.sternotrachealis
M tracheolateralis
M obliquus ventralis
A-I
B-I

Pipromorpha

PLATE 14

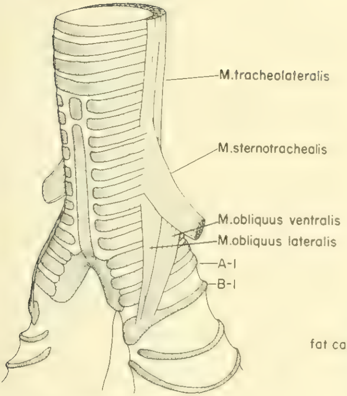
Tyrannidae (V), Dorsal

Colopteryx galeata, dorsolateral view, ×12.

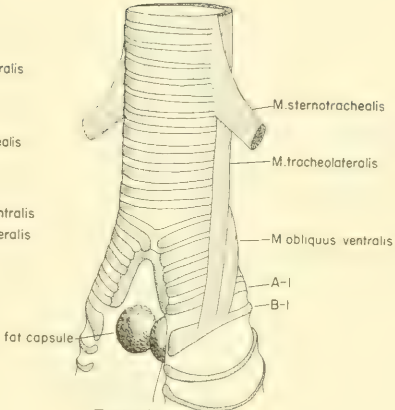
Tachuris rubrigastra, dorsolateral view, ×14.

Elaenia viridicata, dorsolateral view, ×8.

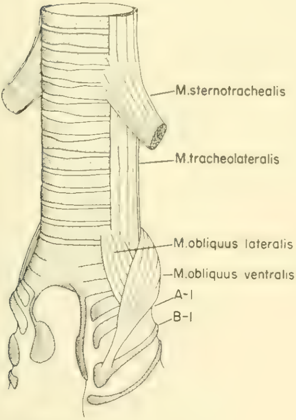
Pipromorpha oleaginea, dorsolateral view, ×9.


M.tracheolateralis
M.sternotrachealis
M.obliquus ventralis
M.obliquus lateralis
A-1
B-1

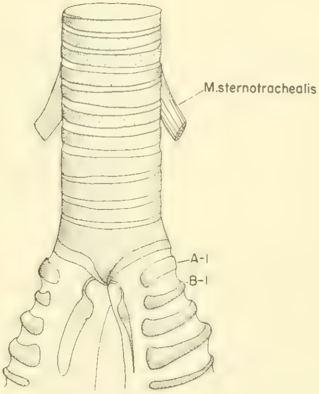
Colopteryx


M.sternotrachealis
M.tracheolateralis
M obliquus ventralis
A-1
B-1
fat capsule

Tachuris


M.sternotrachealis
M.tracheolateralis
M.obliquus lateralis
M.obliquus ventralis
A-1
B-1

Elaenia


M.sternotrachealis
A-1
B-1

Pipromorpha

PLATE 15

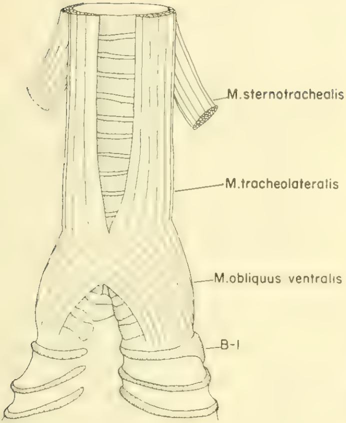
Cotingidae and Pipridae, Ventral

Attila spadiceus, ventrilateral view, ×6.

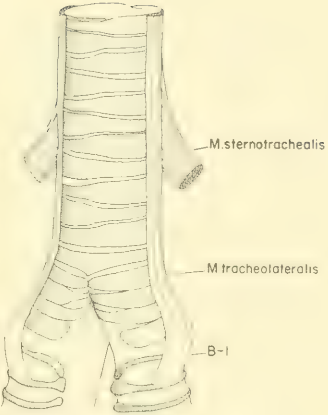
Cotinga amabilis, ventrilateral view, ×6.

Chiroxiphia lanceolata, ventrilateral view, ×8.

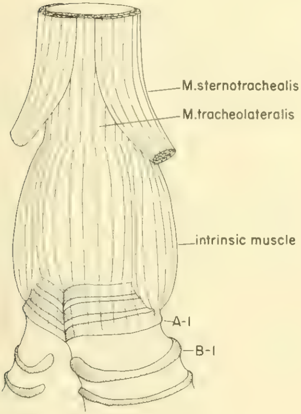
Corapipo leucorrhoa, ventrilateral view, ×9.


M.sternotrachealis
M.tracheolateralis
M.obliquus ventralis
B-1

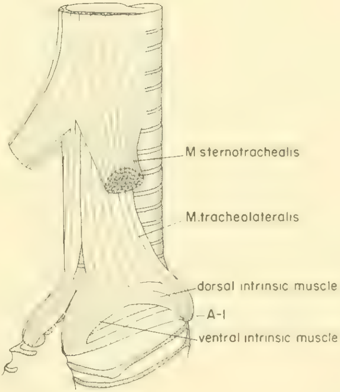
Attila


M.sternotrachealis
M.tracheolateralis
B-1

Cotinga


M.sternotrachealis
M.tracheolateralis
intrinsic muscle
A-1
B-1

Chiroxiphia


M sternotrachealis
M.tracheolateralis
dorsal intrinsic muscle
A-1
ventral intrinsic muscle

Corapipo

PLATE 16

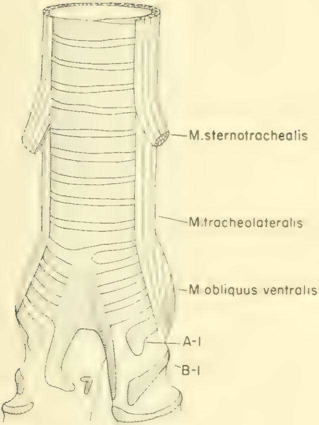
Cotingidae and Pipridae, Dorsal

Attila spadiceus, ventrilateral view, ×6.

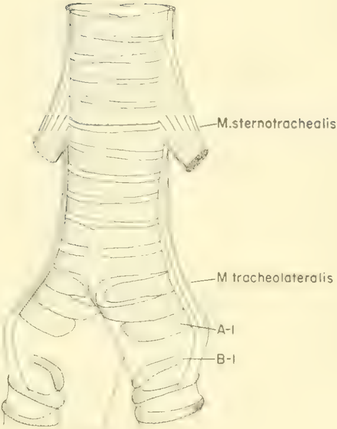
Cotinga amabilis, dorsolateral view, ×6.

Chiroxiphia lanceolata, dorsolateral view, ×8.

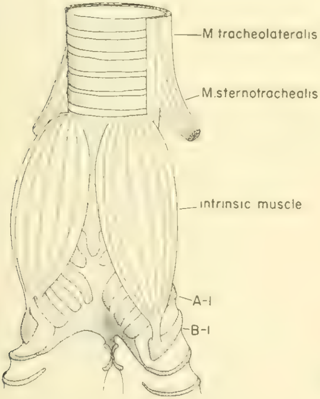
Corapipo leucorrhoa, dorsolateral view, ×9.


M.sternotrachealis
M.tracheolateralis
M obliquus ventralis
A-I
B-I

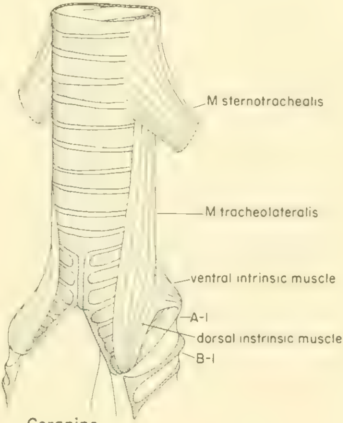
Attila


M.sternotrachealis
M tracheolateralis
A-I
B-I

Cotinga


M tracheolateralis
M.sternotrachealis
intrinsic muscle
A-I
B-I

Chiroxiphia


M sternotrachealis
M tracheolateralis
ventral intrinsic muscle
A-I
dorsal instrinsic muscle
B-I

Corapipo

PLATE 17

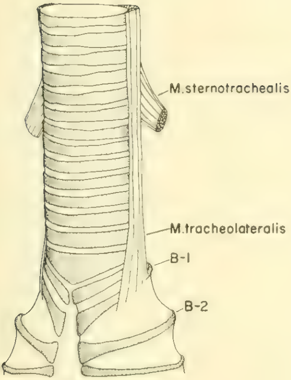
Miscellaneous Families, Ventral

Phytotoma rara, ventrilateral view, ×6.

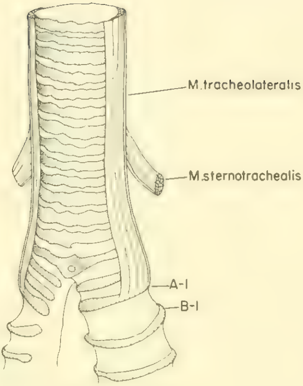
Pitta reichenowi, ventrilateral view, ×6.

Philepitta castanea, ventrilateral view, ×8.

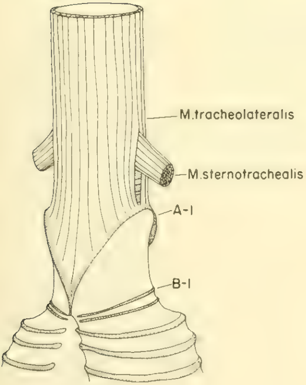
Menura novaehollandiae, ventrilateral view, ×5.


M.sternotrachealis
M.tracheolateralis
B-1
B-2

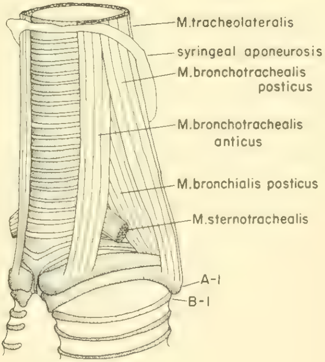
Phytotoma


M.tracheolateralis
M.sternotrachealis
A-1
B-1

Pitta


M.tracheolateralis
M.sternotrachealis
A-1
B-1

Philepitta


M.tracheolateralis
syringeal aponeurosis
M.bronchotrachealis posticus
M.bronchotrachealis anticus
M.bronchialis posticus
M.sternotrachealis
A-1
B-1

Menura

PLATE 18

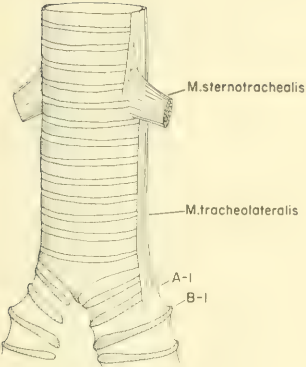
Miscellaneous Families, Dorsal

Phytotoma rara, ventrilateral view, ×6.

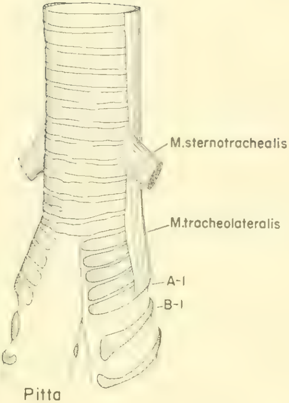
Pitta reichenowi, ventrilateral view, ×6.

Philepitta castanea, ventrilateral view, ×8.

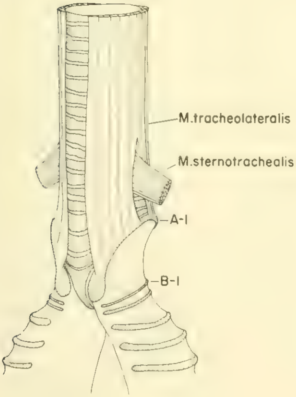
Menura novaehollandiae, ventrilateral view, ×5.


M.sternotrachealis
M.tracheolateralis
A-1
B-1

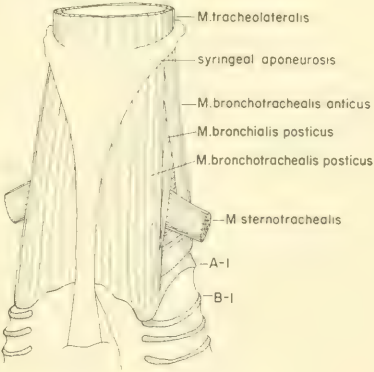
Phytotoma


M.sternotrachealis
M.tracheolateralis
A-1
B-1

Pitta


M.tracheolateralis
M.sternotrachealis
A-1
B-1

Philepitta


M.tracheolateralis
syringeal aponeurosis
M.bronchotrachealis anticus
M.bronchialis posticus
M.bronchotrachealis posticus
M sternotrachealis
A-1
B-1

Menura

PLATE 19

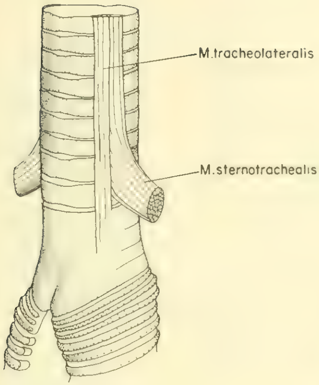
Acanthisittidae and Atrichornithidae

Acanthisitta chloris, ventrilateral view, ×9.

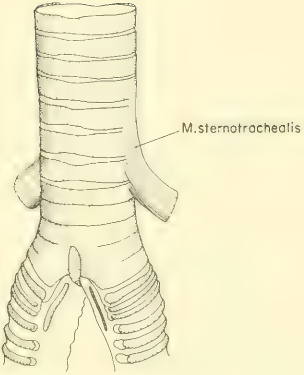
Same, dorsolateral view, ×9.

Atrichornis clamosus, ventrilateral view, ×6.

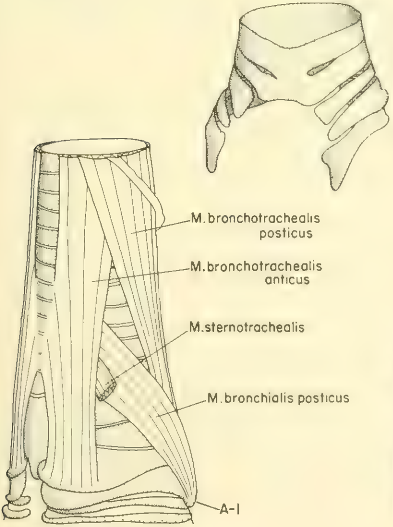
Same, dorsolateral view, ×6.


M.tracheolateralis
M.sternotrachealis

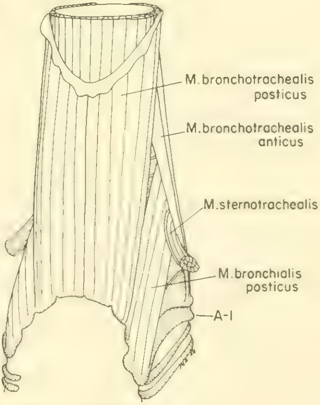
Acanthisitta, ventral


M.sternotrachealis

Acanthisitta, dorsal


M.bronchotrachealis posticus
M.bronchotrachealis anticus
M.sternotrachealis
M.bronchialis posticus
A-I

Atrichornis, ventral


M.bronchotrachealis posticus
M.bronchotrachealis anticus
M.sternotrachealis
M.bronchialis posticus
A-I

Atrichornis, dorsal

PLATE 20

Some Specializations of Lower A-Elements, Reading from Left to Right

Cephalopterus ornatus, A-5R and A-6, ventrilateral view, ×2.5.

Pyroderus scutatus, A-2R, A-2L and A-3, ventrilateral view, ×3.

Phytotoma rutila, A-1R and A-2, ventrilateral view, ×6.

Phytotoma rara, (YPM 2474), A-1R and A-2, ventrilateral view, ×6.

Tityra inquisitor, A-1R, A-2R, A-3, and A-4, ventrilateral view, ×3.

Onychorhynchus coronatus, A-3L and A-4, dorsolateral view, ×8.

Myiophobus fasciatus, A-4L and A-5R, dorsolateral view, ×8.

Heliochera rubrocristata, A-1R and A-2, ventrilateral view, ×3.

Machetornis rixosa, A-1L and A-2, dorsolateral view, ×6.

Capsiempis flaveola, A-1L and A-2 through A-5, dorsolateral view, ×6.

Phylloscartes ventralis, A-2R and A-3, ventrilateral view, ×8.

Mecocerculus leucophrys, A-1L and A-2 through A-4, dorsolateral view, ×6.

Tolmomyias sulphurescens, A-1L, A-2L, A-3L, A-4 and A-5, dorsolateral view, ×8.

Habrura pectoralis, YPM 2659, A-1L, A-2, A-3 and A-3aR, dorsolateral view, ×8.

Colorhamphus parvirostris, A-1L, A-2R and A-3, dorsolateral view, ×8.

Serpophaga subcristata, A-1L, and A-2 through A-5, and left internal cartilage, dorsolateral view, ×8.

Euscarthmus melorhyphus, A-2L and A-3 through A-9, dorsolateral view, ×8.

Pogonotriccus eximius, A-1L, A-2L, A-3 and A-4, dorsolateral view, ×8.

Phaeomyias murina, YPM 2046, A-1L and A-2R through A-4, dorsolateral view, ×8.

Phaeomyias murina, YPM 2038, A-1L, A-2 and A-3, dorsolateral view, ×8.

Stigmatura budytoides, A-1L through A-8 and internal cartilages, dorsolateral view, ×9.

Elaenia caniceps, A-1L, A-2 through A-4, dorsolateral view, ×8.

Neodrepanis coruscans, A-1L and internal cartilages, dorsolateral view, ×9.

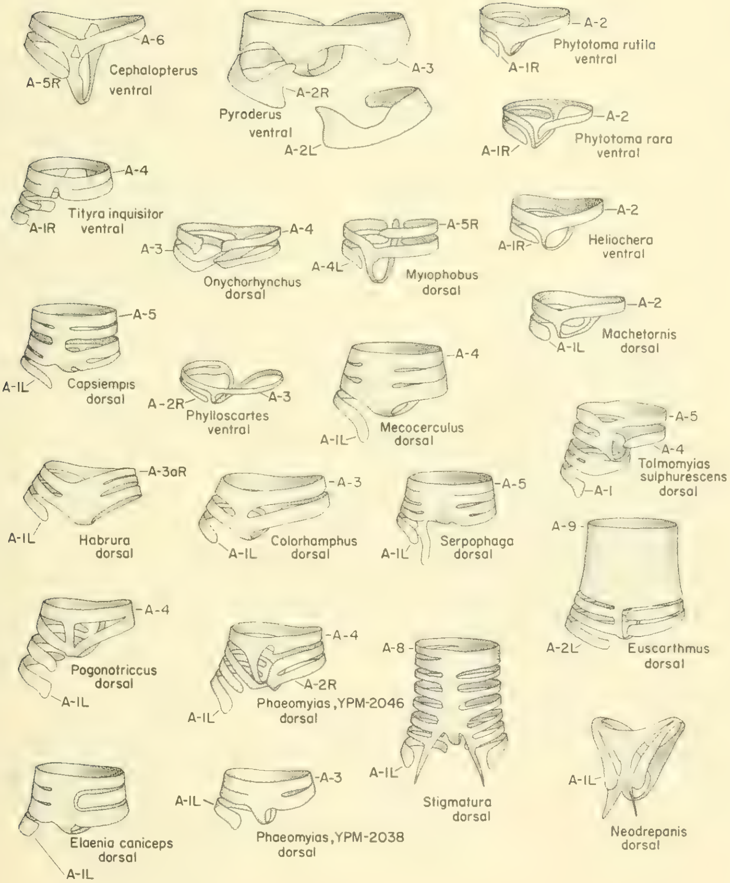

A-6
A-5R
Cephalopterus
ventral
A-3
A-2R
Pyroderus
ventral
A-2L
A-2
A-1R
Phytotoma rutila
ventral
A-2
A-1R
Phytotoma rara
ventral
A-4
A-1R
Tityra inquisitor
ventral
A-3
A-4
Onychorhynchus
dorsal
A-5R
A-4L
Myiophobus
dorsal
A-2
A-1R
Heliochera
ventral
A-5
A-1L
Capsiempis
dorsal
A-2R
A-3
Phylloscartes
ventral
A-4
A-1L
Mecocerculus
dorsal
A-2
A-1L
Machetornis
dorsal
A-5
A-4
A-1
Tolmomyias
sulphurescens
dorsal
A-3aR
A-1L
Habrura
dorsal
A-3
A-1L
Colorhamphus
dorsal
A-5
A-1L
Serpophaga
dorsal
A-9
A-2L
Euscarthmus
dorsal
A-4
A-1L
Pogonotriccus
dorsal
A-4
A-2R
A-1L
Phaeomyias, YPM-2046
dorsal
A-8
A-1L
Stigmatura
dorsal
A-1L
Elaenia caniceps
dorsal
A-1L
A-3
Phaeomyias, YPM-2038
dorsal
A-1L
Neodrepanis
dorsal

PLATE 21

The Oscine Syrinx

(Reprinted, by permission, from A. J. Berger and J.C. George, *Avian Myology,* in which this drawing originally appeared. © 1966 by Academic Press, Inc.)

Fig. 1 *Corvus brachyrhynchus,* ventrilateral view, ×5.

Fig. 2 Same, dorsolateral view, ×5.

Fig. 3 Same, A-1, A-3 and drum, left dorsolateral view, ×3.

Fig. 4 Same, A-3 and drum, left ventrilateral view, ×5.

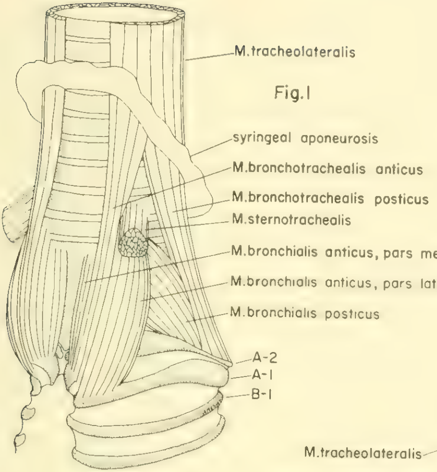

M.tracheolateralis
syringeal aponeurosis
M.bronchotrachealis anticus
M.bronchotrachealis posticus
M.sternotrachealis
M.bronchialis anticus, pars medialis
M.bronchialis anticus, pars lateralis
M.bronchialis posticus
A-2
A-1
B-1

Fig.1

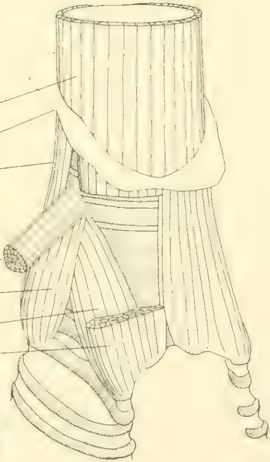

M.tracheolateralis
syringeal aponeurosis
M.bronchotrachealis anticus
M.sternotrachealis
M.bronchialis anticus, pars lateralis
M.bronchialis posticus
M.bronchotrachealis posticus

Fig.2

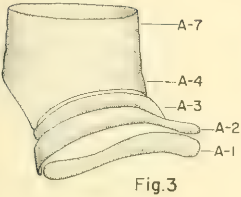

A-7
A-4
A-3
A-2
A-1

Fig.3

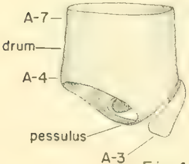

A-7
drum
A-4
pessulus
A-3

Fig.4

The Structure and Relationships of the Primitive Devonian Lungfish — *Dipnorhynchus sussmilchi* (Etheridge)

Keith Stewart Thomson

K. S. W. Campbell

Bulletin 38

PEABODY MUSEUM
OF NATURAL HISTORY
YALE UNIVERSITY

The Structure and Relationships of the Primitive Devonian Lungfish—*Dipnorhynchus sussmilchi* (Etheridge)

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Yale University

K. S. W. CAMPBELL
Department of Geology
Australian National University

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109 P., 95 FIGS., 1971

THE STRUCTURE AND RELATIONSHIPS OF THE PRIMITIVE DEVONIAN LUNGFISH— *Dipnorhynchus sussmilchi* (Etheridge)

KEITH STEWART THOMSON AND K. S. W. CAMPBELL

ABSTRACT

Dipnorhynchus sussmilchi (Etheridge) is an early Emsian-early Eifelian marine Devonian lungfish. The structure of the skull, scales, and portions of the branchial skeleton are described from acid preparations of uncrushed specimens. A detailed examination of the dermal bone patterns and the lateral-line system in *Dipnorhynchus* and comparison with other Paleozoic lungfish allows refinement of the Forster-Cooper system of bone nomenclature. New interpretations of the mandibles of *Dipterus* and *Melanognathus* together with description of the mandible in *Dipnorhynchus* are also made, with some observations on the evolution of the whole head region in Dipnoi. The endocranium of *Dipnorhynchus* is well preserved and shows important differences from that of other known Dipnoi in the oticotemporal region. A unique structure, cautiously identified as an hyomandibula, is present. The scales of *Dipnorhynchus* are extremely similar to those of *Uranolophus* and show certain resemblances to those of Crossopterygii. A new outline scheme of dipnoan evolution is derived from study of a variety of different structural complexes. It is concluded that the Dipnoi show sufficient similarity to the Crossopterygii to warrant their inclusion in a single group Sarcopterygii.

Zusammenfassung

Dipnorhynchus sussmilchi Etheridge ist ein Lungenfisch aus dem Unteren Ems-Unteren Eifel marinen Devon. Der Bau des Kopfes, die Schuppen sowie Teile des branchialen Skeletts wurden beschrieben an Hand von säurepräparierten, unzerstörten Fossilien. Durch eine genaue Untersuchung der Deckknochenanordnung und des Seitenliniensystems des *Dipnorhynchus* im Vergleich mit anderen paläozonischen Lungenfischen wurde es möglich, das Forster-Cooper System der Knockennomenklatur genauer zu definieren. Auch wurden neue Deutungen der Mandibeln von *Dipterus* und *Melanognathus* gemacht sowie eine Beschreibung des Mandibels von *Dipnorhynchus* und einige Bemerkungen zur Evolution der ganzen Kopfregion der Dipnoi. Das Endocranium des *Dipnorhychus* ist gut erhalten und weist wichtige Unterschiede auf im Vergleich mit anderen bekannten Dipnoi in der Otico-Temporal Region. Bemerkenswert ist eine Struktur, die wir hier vorsichtshalber als Hyomandibulare bezeichnen. Die Schuppen des *Dipnorhynchus* sind denen des *Uranolophus* äusserst ähnlich und zeigen auch gewisse Ahnlichkeiten mit denen der Crossopterygii. Eine neue Evolutionstheorie für die Dipnoi basiert auf Untersuchungen einer Anzahl verschiedener Gruppen morphologischer Merkmale. Wir sind der Meinung, dass die Dipnoi genügende Ahnlichkeiten mit den Crossopterygii haben, um sie als selbständige Gruppe Sarcopterygii einzureihen.

РЕЗЮМЕ

Dipnorhynchus sussmilchi Этридж — морская девонская двоякодышащая рыба ранне-эмского или ранне-эйфельского периодов. Структура черепа, чешуи и костяка жабры описаны по кислотным препаратам цельных образцов. Детальное исследование структуры дермальных костей и системы боковых линий у *Dipnorhynchus* и сравнение с другими палеозойскими двоякодышащими рыбами позволяет уточнить систему костяной номенклатуры Форстера-Купера. Приводятся новые интерпретации нижней челюсти у *Dipterus* и *Melanognathus*, а также и описание нижной челюсти у *Dipnorhynchus* с некоторыми наблюдениями об эволюции всей головной области двоякодышащих. Эндокраниум у *Dipnorhynchus* хорошо сохранился и свидетельствует о значительном различии в ушно-височной области между ним и другими известными двоякодышащими. У *Dipnorhynchus* здесь находится единственная в своем роде структура, предварительно определяемая, как гиомандибула. Чешуя у *Dipnorhynchus* очень похожа на чешую *Uranolophus* и имеет некоторое сходство с чешуей группы Crossopterygii. Новая схема эволюции двоякодышащих выводится из исследования различных структуральных комплексов. В заключение констатируется, что сходство двоякодышащих с группой Crossopterygii достаточно велико, чтобы включить их в единую категорию Sarcopterygii.

INTRODUCTION

The lungfishes (Osteichthyes: Dipnoi) have long occupied a special place in the study of evolution. It is well known that the fossil record of the group extends from the Devonian to the Quaternary and that the three living genera are in many ways "living fossils," being little changed from their Mesozoic ancestors. The continuity of the fossil record of Dipnoi has made them ideal subjects for the study of modes and rates of evolution. However, the Dipnoi are of more general importance because of their close anatomical similarity to the Amphibia. When first discovered, they were described as amphibians—a misapprehension soon corrected by Huxley and Lankester. However, the presence of lungs, used in obligate air-breathing in *Protopterus* Owen and *Lepidosiren* Fitzinger, the lobed-paired fins and the structure of the heart and brain, among other features, persuaded many that the Dipnoi constituted the ancestral stock from which tetrapods had evolved. Later the position of honor had to be yielded to the Paleozoic Crossopterygii (specifically the Rhipidistia) and since that time the problem of the precise phylogenetic position of the Dipnoi has been the subject of considerable discussion. As will be noted below, the Dipnoi have normally been closely linked with the Crossopterygii, but this has been contested in recent years. Therefore, whereas the Dipnoi are one of the best-known groups of fishes, many important problems concerning their history remain to be solved.

Recently, due to certain important discoveries, attention has been concentrated on the very early history of the Dipnoi. Up to 1945, the earliest known fossil dipnoan was *Dipnorhynchus sussmilchi* (Etheridge) from the Early to Middle Devonian of Australia. This species was represented by a specimen showing the skull roof and a poorly defined lower jaw (Etheridge, 1906; Hills, 1933, 1936, 1941). In 1945, Lehmann discovered a specimen in the Hunsrückschiefer of Germany that was later described (Lehmann and Westoll, 1952; Lehmann, 1956) as *Dipnorhynchus lehmanni*. This specimen showed the skull roof and part of the palate, although the preservation made the identification of many details uncertain (see later discussion). In 1963, H. A. Toombs of the British Museum (Natural History) collected a detached palate, an almost complete lower jaw, and a second jaw fragment of *D. sussmilchi* in the area from which the holotype had been collected. In 1964, K. S. W. Campbell discovered a second specimen of the skull of *D. sussmilchi* that showed a very well-preserved skull roof and palate. A preliminary description of this specimen was published (Campbell, 1965), and full-scale preparation of the new specimen was started as a prelude to the present more comprehensive treatment. In addition, it was realized that the holotype could also be prepared to show further structures. Ultimately, all the materials of *D. sussmilchi* were assembled by the present authors and prepared. All were found to be essentially uncrushed and preserved in a most remarkably detailed way.

In 1968, Denison (1968a,b) published a description of a new Lower Devonian from *Uranolophus* from the western United States. Although slightly less well preserved in the cranial region than *Dipnorhynchus sussmilchi,* this material has provided extremely important new information concerning the postcranial skeleton of a primitive lungfish.

We present, in the following account, a description of the structure of *Dipnorhynchus* and a reassessment of dipnoan morphology and relationships based on a comparative study of early Dipnoi. In the authorship of this paper, Campbell was largely responsible for the sections involving the skull roof and jaw and Thomson for the braincase and palate. The final version is our joint work.

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MATERIALS AND METHODS

With one exception, the material used in this study has come from the Lower to Middle Devonian limestones of the Taemas district, about thirty miles northwest of Canberra, Australia. The exception is from Buchan in northeastern Victoria, where there outcrops a sequence of rocks similar in lithology, faunal content, and age to those at Taemas (see later discussion).

The first specimen to be described (the holotype, Australian Museum AM F10813A, Etheridge, 1906) was collected by G. A. Sussmilch from a locality given as Portion 44, Parish of Taemas. Browne (1959), however, records that the specimen came from the *Spinella yassensis* Limestone outcrop less than half a mile north of Taemas house. It is not known if it was found loose or *in situ*. The holotype, which was taken to be a skull roof and snout only, was redescribed by Hills (1933, 1941) who, although he did not seek to extract it from the matrix, prepared the lateral-line system on the left side of the skull roof. A small fragment of bone (AM F10813B) in the matrix on the undersurface of the specimen was interpreted as an isolated tooth plate. Through the courtesy of H. O. Fletcher, Curator of Fossils at the Australian Museum, permission was obtained in 1967 to prepare the specimen by acid etching in the Department of Geology, Australian National University. This work was done by J. Bein, using techniques based on those developed in the British Museum (Natural History) by H. A. Toombs and A. E. Rixon (see Toombs, 1959 and Rixon, 1949, for details). It revealed a superbly preserved palate and braincase in almost the natural position beneath the skull roof.

In 1936 Hills described the external dermal bones of a mandible from Buchan, Victoria, as a probable representative of *Dipnorhynchus*. A large part of the external surface had been lost before it came to the National Museum, Melbourne, where it is now housed (P 13837). However, interpretation was possible because an impression of the radiating structure of the internal surfaces of the dermal bones had been left on the matrix filling the Meckelian vacuity. Permission was obtained from E. D. Gill, Deputy Director of the National Museum, to prepare this specimen by acid etching after the above-mentioned structures had been recorded in plaster casts. Not only were the internal elements of the mandible found to be almost complete and uncrushed, but the cavities of the jaw contained a large cheek plate (P 13837A, National Museum), several scales (P 13837B-F), and a portion of the branchial apparatus (P 13837G). Neither the exact locality nor horizon of this specimen is known. Attempts to identify the horizon by recovering microfossils from the acid residues were unsuccessful.

In 1963, Toombs visited the Taemas area and collected three specimens in loose rocks; because of the nature of the weathering and topography it is possible to fix their provenance within narrow limits. These specimens were all prepared by acid etching in the British Museum (Natural History) and are now in the collections of that institution. The first specimen (P 33699) is the greater part of a palate with a detached snout, from the Bloomfield or *Receptaculites* Limestones about ½ mile west-southwest of Taemas Bridge. It is undescribed, but White (1965, p. 36) referred to the character of its dentition. The other two specimens are mandibles. One (P 46773) is almost complete, lacking only some of the dermal bone on the left side. It was found on the right bank of the Burrinjuck Dam, 2,500 yards east of Majurgong trig., and is almost certainly from the *Spinella yassensis* Limestone. The other specimen (P 33714) was found approximately 1,950 yards on a bearing 352° magnetic from the Bloomfield Homestead and is probably from the Bloomfield Limestone. Both of these mandibles were mentioned by White (1965, p. 39) and P 33714 was sectioned to provide the histological data given by that author in a more recent paper (White, 1966; p. 7, pl. 1, fig. 1).

Isolated scales from the same area were collected by J. A. Warren, Monash University (1970D and thin-section 2931–Zoology Department Collections).

In 1965 an almost complete skull was discovered at the locality known as Shearsby's Wallpaper, Taemas, in the *Spinella yassensis* Limestone (see Campbell, 1965). This specimen has also been etched in acid. The braincase is less complete posteriorly than that of the holotype, but the skull roof is almost entire. It is now cataloged as 18815 in the Geology Department Collection, Australian National University. These specimens are illustrated in Figures 1 to 35 and in numerous photographs (Figures 36 to 95).

ABBREVIATIONS USED

acv	anterior cerebral vein
alc	anterolateral chamber of nasal organ
amc	anteromedian chamber of nasal organ
amt	anteromedian tuberosity
an	position of anterior naris
ang	angular
ant f	anterior furrow
ant pt	anterior pterygoid
aoa	anterior ophthalmic artery
art	articular
bb 1, bb 2	basibranchials 1, 2
c b VII	canal for n. buccalis VII
c ea I	canal for first efferent branchial artery
c ep	cavum epiptericum
c hy VII	canal for r. hyomandibularis VII
c int ca	canal for internal carotid artery
c j	canal for jugular vein
c m V (cc m V)	canals for r. maxillaris V
c mcv	canal for median cerebral vein
c o a	canal for orbital artery
c oph a	canal for anterior ophthalmic artery
c os VII	canal for r. ophthalmicus superficialis VII
c ot VII	canal for r. oticus VII
c pal a	canal for palatal artery
c pal VII	canal for r. palatinus VII
c pit v	canal for pituitary vein
c prf	canal for r. profundus V
c II	canal for optic nerve
c III	canal for third cranial nerve
cc	canals in dermal bone
cer md lig	insertion of ceratomandibular ligament
ch	vascular chamber posterior to Meckelian vacuity
cor	coronoids
d	dentary
dl cr	dorsolateral crista
dm cr	dorsomedian crista
f ch	foramen in posterior wall of Meckelian vacuity
f_1 ea–f_2 ea I	foramina for first efferent branchial artery
f int V	foramen for r. mandibularis internus V
f m ll	foramen for mandibular lateral line
f md V	foramen for mandibularis V
f me VII	foramen for r. mentalis externus VII
f_1 mi VII–f_2 mi VII	foramina for r. mentalis internus VII
f o a	foramen for orbital artery

f o ll	foramen for oral lateral line
f oph a	foramen for ophthalmic artery
f pal VII	foramen for r. palatinus VII
f prf	foramen for r. profundus V
f_1 sa I–f_2 sa I	foramina for superior branch of first efferent branchial artery
fv?	possible vascular foramina
g pr	process for m. geniocoracoideus
gl	glenoid fossa
gr ea I	groove for first efferent branchial artery
gr int ca	groove for internal carotid artery
gr j	groove for jugular vein
gr l	groove for lateral aorta
gr m V + VII	groove for r. mandibularis V and VII
gr me VII	groove for r. mandibularis externus VII
gr mi VII	groove for r. mentalis internus VII
gr subn v	groove for subnasal vein
hb 4, hb 5	hypobranchials 4 and 5
hy VII	(canal for) r. hyomandibularis VII
hyp	cavity for hypophysis
hyp r	hypophysial recess
int ca	(canal for) internal carotid artery
int pr	process for intermandibularis muscle
l p lr	lateral palatal process
lab p	labial pit
lgr	lateral groove (palate)
lr	lateral ridge (palate)
lt	lateral tuberosity (palate)
Mck b	Meckelian bone
Mck f	Meckelian fossa
Mck v	Meckelian vacuity
mcv	medial cerebral vein
mll	mandibular lateral-line canal
mm V	foramen for combined rami maxillaris-mandibularis V
mtd	median transverse depression (palate)
mv	maxillaris ramus of fifth nerve
nch	notochord
oll	oral lateral-line canal
op	operculum
op pr	opercular process of hyomandibula
ot VII	(canal for) r. oticus VII
p c	posterior chamber of nasal cavity
p md l	shelf for palatomandibular ligament
p n	position of posterior naris
p st	stalk of parietal organ
pch	"parachordal"

pit v	(canal for) pituitary vein
pmel	posteromedian elevation (palate)
pn w	postnasal wall
pr art	prearticular
pra t	prearticular tubercle
prf V	(canal for) r. profundus V
prg p	preglenoid process
psp	postsplenial
r	ridge
r a mm	ridge for adductor mandibulae muscles
r os VII	r. ophthalmicus superficialis VII
s n	solum nasi
sang	surangular
sa I	groove for superior branch of first efferent branchial artery
sl	sulcus
sp	splenial
sp r	spiracular recess
t p	tooth plate
tt	rostral tubuli (schematized in Figs. 21, 22)
uh	urohyal
vc?	unidentified vascular canals
II	foramen for optic nerve
III	foramen for third cranial nerve
IV	foramen for fourth cranial nerve
X (IX)	foramina for tenth cranial nerve

ENVIRONMENT OF *DIPNORHYNCHUS SUSSMILCHI*

All known specimens of *Dipnorhynchus sussmilchi* have been found in marine limestones and associated with an abundant and diverse fauna of brachiopods, corals, bivalves, nautiloids, polyzoans, etc.

Hills (1941) and Campbell (1965) concluded that the fish were marine, but several people have questioned this in discussion and suggested that they were carried in by streams. This matter requires examination because of its physiological and phylogenetic implications, especially as the only other known species of the genus, *D. lehmanni,* was also recovered from a marine formation, the Hunsrückschiefer of Germany.

Dipnorhynchus is not the only fish to occur in the Buchan, Taemas, and Wee Jasper limestones. There are several species of placoderms, of which the arthrodires *Williamsaspis bedfordi* White, *Buchanosteus murrumbidgeensis* White, *Taemasosteus novaustrocambricus* White and *Notopetalichthys hillsi* Woodward are the only ones described (White, 1952).

At Taemas, dermal bones of these fishes have been found in every unit from the Cavan Bluff Limestone to the Warroo Limestone, with the exception of the Majurgong Shale. They are not common and usually occur randomly distributed, but occasionally one finds relatively thin limestone units in which they are more abundant than normal; for example, at places in the Warroo Limestone, and at Cave Flat, near Burrinjuck, where about 70 completely or partly disarticulated fragments of dermal shields were collected in an outcrop 100 yards long and 20 feet thick. In this latter outcrop a well-preserved dipnoan skull was also collected, together with two small fragments of dipnoan bone. The bones are usually separated by at least several meters, never show signs of having been washed together, and are randomly oriented.

Although the placoderm shields are invariably partly or completely disarticulated and the dipnoan skulls have lost their cheek plates, the remains show little or no signs of physical transport. The surface detail is well preserved and there is little or no abrasion. This, together with the type of distribution mentioned above, suggests that the disarticulation is more likely to be the result of predation. The predators could be either large nautiloids, the remains of which are common, or the arthrodires, or both.

This interpretation of little transport is supported both by the character of the enclosing sediments themselves and by the preservation of the associated invertebrates. The specimen from Shearsby's Wallpaper came from a bed containing a profusion of the brachiopods ?*Protochonetes culleni* (Dun) and *Spinella yassensis* (de Koninck), most of which retain their valves articulated, and many of which are either in living position or just rolled over. The finest of details are preserved—for example, the cardinal spines on the chonetids and the microscopic spinules that cover both valves of the spiriferids. An assemblage of this sort requires conditions too quiet to permit the transport of a *Dipnorhynchus* skull along the sea bottom. Other specimens come from sediments indicative of rather more turbulent conditions, but in general all occurrences could be categorized as being in low-energy environments. It is quite unrealistic, therefore, to suggest that these fossils were washed in as skeletons.

However, none of the above arguments precludes the possibility that the fish were washed in alive or as bloated cadavers by rivers in floods, that they were predated in the sea with their remains falling to the bottom to be moved slightly by bottom currents before final burial. The following points can be urged against this view:

1) The limestones usually contain less than five percent of terrigenous material. On solution in acid they produce only silicified fossils and a black organic sludge, which is usually free of silt. It is true that in the *Spinella yassensis* Limestone there are numerous thin interbeds of silt and mud, which are probably of terrigenous origin, but the fish remains are in the limestone rather than in the silty sediments.

2) The associated marine fauna is rich and diversified. Many of the fish plates come from beds rich in well-preserved corals, stromatoporoids, articulate brachiopods, and fenestellid polyzoans—all of which were sensitive to turbidity and low salinity. One would expect that streams bringing in heavily armored fishes would also carry quantities of mud and be of sufficient volume to lower the salinity considerably.

3) Algae are common throughout the limestones and must have made an important contribution to their bulk. These and the associated fauna indicate a shallow-water marine platform environment.

All these features suggest that any streams debouching into the area from possible neighboring land must have been carried in very narrow channels across the limestone flats, or had very low discharge rates, or both. To date no such channels have been recognized. In the unlikely event of fish being brought down such channels and spread out from them by predators or by swimming before they died, there should be some evidence of other floating debris from the land. Vascular plants, for example, were in existence at this time as is proved by their occurrence in the Kirawin Shale, lower in the sequence in the Taemas-Wee Jasper region; yet they are very rare or absent from the limestones. In assessing the probability of such a mechanism for introducing the fish, it must be kept in mind that Buchan is about 180 miles south of Burrinjuck, which is 15 miles west of Taemas, and that it is not only one but some hundreds of occurrences of fish remains at several stratigraphic levels that have to be accounted for.

Finally, the anatomy of *D. sussmilchi* itself argues in favor of a marine origin. Its "teeth" consist of three bulbous masses anteriorly and a pair of large almost flat palatines, in addition to which the lateral edges of the palate moved against the rounded edges of the prearticulars. There are no sharp teeth that could hold struggling prey. The palate itself is very thick and to judge from the areas of insertion the adductor mandibulae must have been very large. These features taken in conjunction suggest a diet of passive (or dead) but well-protected epifaunal organisms that had to be cracked open and crushed to extract the soft body. Brachiopods, bivalves, gastropods (or possibly dead placoderms) fit these specifications admirably, and they occur in abundance in most of the fish-bearing strata. On the other hand, no such invertebrates are known to occur in Devonian freshwater sediments though freshwater placoderms of this age are known elsewhere in the world.

The balance of evidence indicates that a marine origin for the fish fauna, including *D. sussmilchi,* seems much more probable than a nonmarine origin.

AGE OF THE SPECIMENS

The limestones in all three areas from which specimens were obtained have, until recently, been regarded as either late Early Devonian or early Middle Devonian. Hill (1941), working with corals, concluded that the Cavan Bluff Limestone was probably "somewhere near the base of the Couvinian, or perhaps the top of the Coblenzian." Hills (1941) used this determination in his paper on *Dipnorhynchus*. In 1951, Hill again using corals, concluded that the Buchan Caves Limestone fauna was "near the junction between the Emsian and Couvinian, probably Couvinian." The later units at Buchan were regarded as definitely Couvinian. On the basis of ammonoid and bactritid studies Teichert (1948) concluded that the Taravale Mudstone at Buchan was Eifelian in age, thus apparently confirming the work of Hill. These determinations were accepted by Browne (1959) and Teichert and Talent (1959) in their revisions of the stratigraphy of the Murrumbidgee and Buchan areas and were only slightly modified by Talent (1965b) and Brown, Campbell, and Crook (1968) in surveys of regional stratigraphy.

In a long series of papers Philip and Pedder (1964, 1967b, 1968), Pedder (1964, 1968), Philip (1966), Philip and Jackson (1967), and Pedder, Jackson, and Philip (1970) have disputed this interpretation, largely on the basis of a restudy of the corals by Pedder and an examination of the conodonts by Philip and Jackson. Their work has been accepted without comment by two workers on the vertebrates from these areas (White, 1965; Schultze, 1968), the one quoting a Siegenian and the other a late Emsian age for the same rocks, as a result of the relatively rapid evolution of the views of these authors. A brief review of the present position is therefore warranted, especially as Philip and Pedder, even in their latest work (1968, p. 1027), cite the occurrence of *Dipnorhynchus* as evidence of a Siegenian age.

Certain warnings need to be sounded. High precision correlation of the rocks in the interval at issue is not straightforward. The faunas of the upper Emsian are, in general, more closely related to those of the Eifelian than the lower Emsian, making the definition of the Emsian-Eifelian boundary difficult. Ammonoids, which have been widely regarded as reliable age indices, are rare and little differentiated. Conodonts, which give promise of more refined correlations, remain to be adequately tested and seem to show marked provincialism. For example, icriodids, which are abundant in the northern hemisphere at this time and are used for zonation, are very rare in eastern Australia. Further, species that were thought to be reliable guides are now appearing out of sequence even in adjacent regions; for example, compare the range zones of *Spathognathodus bidentatus* and *Polygnathus kockeliana* in the Harz and Couvin areas (Wittekindt, 1965; Bultynck, 1968).

In addition, there are local facies and biogeographic problems peculiar to southeastern Australia, particularly in connection with coral distribution. For example, *Calceola* occurs in abundance at Bindi in limestones equivalent to the top of the

Buchan Caves Limestone and lower Taravale Formation at Buchan, only 35 miles distant. Yet despite the fact that the facies and the brachiopod faunas are similar, *Calceola* is apparently absent from Buchan. Such examples could be multiplied. In the light of such facts, it would be most remarkable if the Lower-Middle Devonian boundary could be precisely fixed in most sections in eastern Australia at the present time.

As shown above, most of the dipnoans come from the *Spinella yassensis* Limestone to the *Receptaculites* Limestone equivalents. The scales found by Warren are most probably from the Cavan Bluff Limestone. The horizon at Buchan is unknown. The best approach to the discussion of the age of the dipnoans therefore seems to be to examine the limits within which they can be dated.

Most workers would now accept that the Cavan Bluff Limestone is the oldest unit involved. The fauna described from it is sparse and largely endemic. It was reviewed by Philip and Pedder (1968, p. 1032). The only corals also known overseas are *Embolophyllum* and *Tipheophyllum*. According to Pedder the former genus is known elsewhere only from the Keyser Limestone of Gedinnian? age in Maryland where it is represented by a species remote from *Embolophyllum aequiseptatum* (Hill), the Cavan species. *Tipheophyllum bartrumi* (Allan) from Cavan, however, is known also from New Zealand in the Reefton Limestone that lies above the late Siegenian or early Emsian Reefton Mudstone (Boucot et al., 1963). The only other species relevant to the present discussion is the conodont *Polygnathus linguiformis dehiscens* Philip and Jackson. Out of Australia *P. linguiformis* is not known below the Emsian, but Philip and Jackson (1967) regard their subspecies as primitive and therefore indicative of a possible Siegenian age. This evolutionary argument awaits stratigraphic confirmation. The similarity between *P. linguiformis dehiscens* and *P. lenzi* Klapper (1969) from what is regarded as lower (but not basal) Emsian of the Yukon and Nevada suggests that confirmation is unlikely. We conclude that no compelling evidence has yet been put forward favoring a pre-Emsian age for the Cavan Bluff Limestone.

The oldest fossiliferous rocks at Buchan belong to the Buchan Caves Limestone. Philip (1966) regarded them as probably late Siegenian in age because they lacked *Polygnathus linguiformis*, though Philip and Pedder (1967b, 1968) later qualified this opinion, pointing to the difficulty of recognizing the Siegen-Ems boundary in Australia. The Buchan Caves Limestone contains the *Chalcidophyllum recessum* Fauna, which also occurs in the Currajong Limestone in the Taemas area, some 400 feet above the Cavan Bluff Limestone. The Buchan Caves Limestone is unlikely therefore to be older than early Emsian if the above argument is correct. The *Chalcidophyllum recessum* Fauna contains no described elements that are useful for worldwide correlation. However, the beds overlying it apparently without a break at Buchan, the Pyramids Member of the Taravale Mudstone, contain the bactritid and ammonoid faunas originally described by Teichert (1948). The reviews of bactritid and ammonoid distribution in the Lower Devonian throughout the world by Erben (1953, 1960, 1964, 1965) have shown that it is difficult to use the bactritids for fine stratigraphic correlation, and that *Teicherticeras* encompasses a group of species with a wide morphological range. The Buchan species *T. desideratum* (Teichert), *T.* sp. *D* Erben and *T.* sp. *F* Erben do not resemble the late Siegenian or early Emsian species elsewhere. On the contrary, the little evidence available suggests that the greatest similarities in coiling, whorl profile, ornament pattern, and suture shape are with species like *T. lissovi* Bogoslovskiy, the age of which is regarded as late Emsian on the basis of the associated ammonoids (Bogoslovskiy, 1963). In addition, *Talenticeras* is regarded by Erben as an offshoot from *Mimosphinctes*, showing regressive tendencies. However, he was under the impression that the local succession indicated an Eifelian age. This line of argument, like that concerning the Siegenian age of *Polygnathus linguiformis dehiscens* Philip and Jackson, is weak and in need of stratigraphic support. At present the ammonoids seemingly cannot be used to give a precise date, but the weight of evidence is against the view that the *Teicherticeras*-bearing beds of the Taravale Formation are basal Emsian as indicated by Philip and Pedder (1967b, p. 235 and text-fig. 1) or "early, though not necessarily earliest, Emsian" (Philip and Pedder, 1968). The underlying Buchan Caves Limestone cannot be dropped into the Siegenian on this ammonoid evidence.

The occurrence at Bindi of *Calceola sandalina* in abundance with brachiopods of the same type as those occurring with the ammonoids at Buchan supports this view. *C. sandalina* has not been reliably reported from pre-upper Emsian strata anywhere overseas, the oldest occurrence being in the Chapel Limestone of the Zlichovian in Czechoslovakia (Strusz, 1970). Recently Hill and Jell (1969b) have referred *Rhizophyllum calceoloides* Talent from the Kilgower Member of the Tabberabbera Formation in Victoria to *Calceola*. The Kilgower Member has been dated as probably Emsian by Talent, but is considered to be more probably middle Siegenian by Philip and Pedder (1968). However, *C. calceoloides* is acknowledged to have several characters atypical of the genus (see also Talent, 1963); Hill and Jell note that forms with similar morphology occur in the Eifelian *Calceola* beds of the Urals and in the ?Emsian of North Queensland. It seems most reasonable to conclude that the Buchan Caves Limestone can be no older than early Emsian and is more likely to be no older than the middle part of the Emsian. The absence of *Polygnathus* is to be explained either by facies or by incomplete sampling or both. Only three of Philip's samples contained conodonts, and one of these yielded just one specimen.

The youngest rocks containing dipnoans belong to the *Xystriphyllum mitchelli* Fauna of Philip and Pedder (1967b). In its characteristic development this fauna lies above the *Teicherticeras*-bearing beds at Buchan, though there is apparently some overlap in range; it appears about 400 feet above the *Chalcidophyllum recessum* Fauna at Taemas. It contains one of the richest invertebrate faunas in the region. Among the nonendemic corals there are few genera that are not long ranging. None demands an Early Devonian age but, as has been pointed out, the presence of *Acanthophyllum* suggests that it cannot be older than late Emsian (Philip and Pedder, 1967b, p. 235; 1968, p. 1032). The brachiopods *"Spirifer" yassensis*, *"Nadiastrophia," Cymostrophia*, and *Mutationella* have been cited as indicating an Early Devonian age (Philip and Pedder, 1964). *"S." yassensis* is a species of the Emsian to Eifelian genus *Spinella* Talent and is not closely related to the Early Devonian New Zealand genus *Mauispirifer*. The *"Nadiastrophia"* is presumably *Malurostrophia* Campbell and Talent, which is represented by several species in Victoria and New South Wales, and in the Eifelian or possibly late Emsian Ukalunda Beds of Queensland (Campbell and Talent, 1967). It is unknown out of Australia. *Cymostrophia* is not a Lower Devonian index, representatives being found in the Eifelian in the USSR in the Salair Range and the Altai Mountains, and in North America. B. D. E. Chatterton of the Australian National University, who has been studying the brachiopod and trilobite faunas of the *Receptaculites* and Warroo Limestones, informs us that he has been unable to find species of *Mutationella,* though other closely related terebratuloids are present. It is true that the occurrence of a species of *Parachonetes* Johnson close to *P. macrostriatus* (Walcott) suggests a late Emsian age, but against this must be weighed *Quadrithyrina* Havlíček, which is known only from the Eifelian of Czechoslovakia and the Urals; *Spinulicosta* Nalivkin, the only Lower Devonian occurrence of which is in the late Emsian of Nevada (Johnson, 1968) but which occurs in abundance in both Asia and America in the Middle Devonian; and *Cyrtinopsis* Scupin which ranges from the Gedinnian to the Givetian, but is represented at Taemas by a species similar to the late Emsian-Eifelian *C. undosus* (Scheer) and *C. undosus maiderensis* Drot from the Eifelian of Morocco. None of the other brachiopods being studied is limited to the Lower Devonian. We conclude therefore that the members of this group are a mixture of late Emsian and Eifelian forms, and that it would not be unreasonable to suggest on the basis of this evidence that the *Xystriphyllum mitchelli* Fauna crosses the Emsian-Eifelian boundary.

The trilobites give little indication of age. *Acanthopyge (Mephiarges) bifida* Edgell is clearly related to *A.* (*M.*) *mephisto* Richter and Richter from the Eifelian, but is just as close to *A.* (*M.*) *consanguinea* Clarke from the Gedinnian. A species of *Phacops* is at a similar evolutionary level to members of the *Phacops fecundus degener* group that ranges from the late Emsian to the early Eifelian. The occurrence of *Gravicalymene* may be thought to indicate an Early Devonian age, but a similar large species occurs in the Eifelian Imachinsk Suite of the Transbaikal region, USSR (Modzalevskaya, 1968).

The remaining published evidence concerns the conodonts. Philip (1966) and Philip and Jackson (1967) have argued strongly that the occurrence of such species

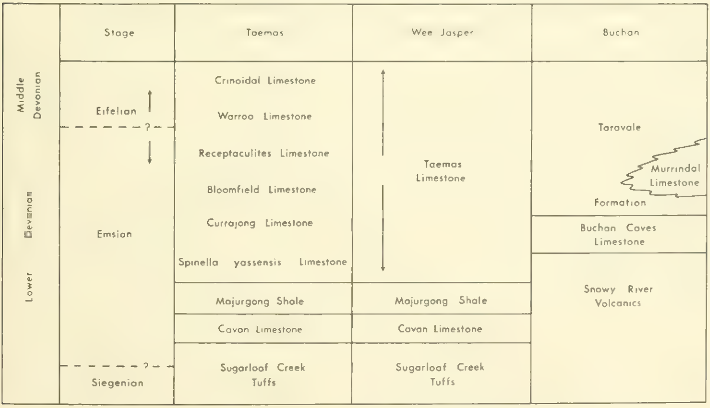

Stage
Taemas
Wee Jasper
Buchan
Middle Devonian
Eifelian
?
Crinoidal Limestone
Warroo Limestone
Receptaculites Limestone
Bloomfield Limestone
Currajong Limestone
Spinella yassensis Limestone
Taemas Limestone
Taravale
Murrindal Limestone
Formation
Lower Devonian
Emsian
Buchan Caves Limestone
Snowy River Volcanics
Majurgong Shale
Majurgong Shale
Cavan Limestone
Cavan Limestone
?
Siegenian
Sugarloaf Creek Tuffs
Sugarloaf Creek Tuffs

FIG. 1. Stratigraphical correlation of the geological sequences in which *Dipnorhynchus sussmilchi* and associated faunas have been found.

as *Ozarkodina typica denkmanni* Ziegler, *Plectospathodus alternatus* Walliser, *Spathognathodus inclinatus* (Rhodes) and *Trichonodella inconstans* Walliser, indicate that the *Xystriphyllum mitchelli* Fauna cannot be younger than late Emsian, and further that it is not latest Emsian. However, all of these species are generalized long ranging types; it would be surprising if their terminal occurrences were contemporaneous the world over. More significant is the occurrence of *Polygnathus linguiformis foveolatus* Philip and Jackson with *P. linguiformis linguiformis* in the top of the fauna apparently without the distinctive Eifelian species of *Polygnathus*. The absence of icriodids hinders solution of this problem.

The conclusion we reach from data at present available (Fig. 1) is that *Dipnorhynchus sussmilchi* occurs in rocks no older than early Emsian and no younger than early Eifelian. Further work on ostracods, tentaculitids, and such brachiopod groups as the rhynchonelloids is needed to reach more precise conclusions.

THE SKULL ROOF OF PALEOZOIC DIPNOI

DEFINITION OF THE DERMAL BONES

In large part, as will be seen in later discussion, interpretation of the phylogeny of Dipnoi depends upon a detailed investigation of the homology of the dermal bones of the skull roof. It is well known (e. g., Westoll, 1949; White, 1966) that the dermal-roofing pattern of Dipnoi is different from that of other groups of fishes, but is fully consistent within the Dipnoi. Forster-Cooper (1937), Romer (1936), Westoll (1949), and White (1965) have been the principal contributors to our understanding of the homology of the dipnoan skull roof, which has developed with the aid of the elegant system of notation developed by Forster-Cooper. The fact that *Dipnorhynchus* shows a more complicated (and presumably more primitive) skull roof pattern than that of *Dipterus*—the genus upon which previous studies have been based—has caused us to re-evaluate the general situation concerning dermal bone patterns in Dipnoi. A first step in such a task is the development of a comprehensive set of definitions for the dermal elements. In preparing such definitions there are several requirements that must be met.

1) A means of tackling the problems of fusion, or invasion, or both must be provided. We have accepted Parrington's view (1949, 1956, 1967; see also White, 1966) that fusion of bones should not be postulated on topographic evidence alone. There seem to be only two other independent lines of approach to the recognition of fused elements. The first of these is the presence of more than one center of ossification, a phenomenon that is only rarely observed. The second concerns only bones on which two lateral-line canals, or a lateral-line canal and a pit line, join. It is best illustrated by reference to the K and X bones of *Dipterus* and *Scaumenacia*. The normal situation in *Dipterus* is represented in Fig. 2A. In Fig. 2B the shape of the bone suggests fusion; this is confirmed by the relative positions of the lateral-line canals. Ossification must have been initiated at both canal junctions. The canals in *Scaumenacia* shown in Fig. 2C indicate a single center of ossification and thus illustrate the capture of the canal issuing from "J" by bone "X," which is not compound. Bone "K" has been eliminated.

Where neither of these situations can be established, we have assumed space capture by one of the adjacent bones; which bone it is not always possible to determine. Some of the problems are outlined subsequently.

2) Criteria for the recognition of homologous structures must be agreed upon. Most work in the field is based upon topographical interrelationships and relations to lateral-line canals and pit lines (for summary see Westoll, 1949; Parrington,

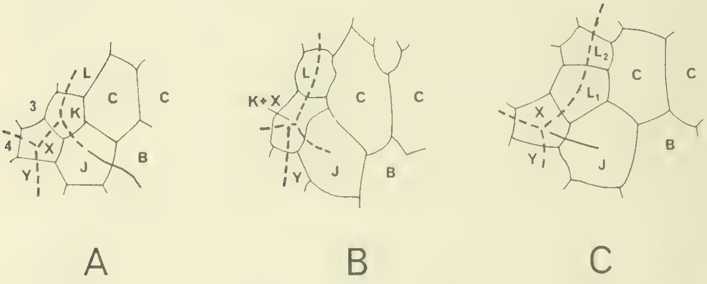


FIG. 2. Portion of the left side of the skull roof in three specimens of Devonian Dipnoi, showing variation in dermal bone pattern. A) *Dipterus valenciennesi*, "normal situation," specimen 33165, British Museum (Natural History); B) *Dipterus valenciennesi*, specimen showing possible fusion of X and K and subsequent modification of the lateral-line canal pattern, specimen 33165, British Museum (Natural History); C) *Scaumenacia curta*, "normal condition" showing that in this case bone K has been eliminated, specimen E 2853, Park Museum. Redrawn from Westoll (1949) and White (1965).

1956 and 1967). We would like to re-emphasize the importance of relation to the structures of the chondrocranium, particularly in the identification of the posterior roofing bones.

3) A standard for the comparison of dermal bone patterns must be established. In the past the skull roof of *Dipterus* has been used as a standard, following the work of Forster-Cooper (1937). However, *Dipnorhynchus sussmilchi* (and also *Uranolophus)* presents a more complex pattern that is both geologically and phylogenetically more primitive. Bones unknown in *Dipterus* now have to be named. Moreover, since the Forster-Cooper system of notation can be adapted to *Dipnorhynchus* with only minor modifications, and since a comparative study of *Dipnorhynchus* helps clear up certain problems in the interpretation of *Dipterus* itself and other forms (see below), we choose *Dipnorhynchus* as a new basis for comparison.

4) An integrated sequential system of analysis should replace the current *ad hoc* approach to the identification of bones. That is, using a given bone as a primary reference point, other bones should be defined in sequence; each definition must be cast only in terms of entities defined earlier in the sequence.

5) The initial reference bone must be one that can be readily recognized in all genera, is not the subject of argument about fusion or splitting, and provides a starting point for a sequence that will extend to all or most of the other bones. Bone "B" satisfies these requirements best.

6) A knowledge of the phylogeny of the group is desirable but is not yet available. On the other hand, the stratigraphic succession of genera is known, and this information is adequate for present purposes.

The definitions that follow (see also Fig. 3) aim at satisfying these requirements. When qualification is necessary, it is clearly indicated.

Bone "B" is the median bone lying over the posterior part of the braincase, anterior to the occipital commissure of the lateral-line canal, and either carrying the ends of the anterior pit lines or lying between them.

Bone "I" can then be defined as an element carrying the posterior pit line, in contact with the posterolateral margin of B, and supported on its ventral surface by the dorsolateral crista of the braincase.

"A" is a median bone carrying the occipital commissure, in contact with "I" on its anterolateral edges, and usually also in contact with "B." It lies behind the median crista of the braincase and is loosely attached along its anterior and lateral edges.

Bones "C" are paired bones immediately anterior to "B." They may be fused medially as an individual variation *(Dipnorhynchus)*.

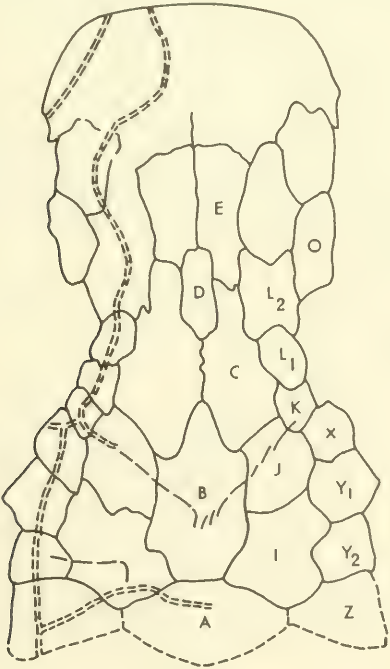


FIG. 3. *Dipterus valenciennesi*, skull roof showing "normal" arrangement of dermal bones and lateral-line system. Redrawn from White (1965) with bones labelled according to the system developed here. Specimen P 7834, British Museum (Natural History).

In the bone series anterior to "C" there are at present no clearly defined reference points that enable homologies to be decided. The position of the pineal foramen, or where that is not present the pineal stalk, offers a possible solution to part of the difficulty, but the problems involved are great. They are later discussed under *Soederberghia.*

Bone "J" lies immediately in front of "I" and lateral to "B," carries the anterior pit line and, in the more primitive genera, the posterior end of the supraorbital lateral-line canal from which the anterior pit line evolved.

Bone "X" has a contact with the anterolateral or the lateral edge of "J" and contains the junction between the main and the infraorbital lateral-line canals.

Posterior to "X" is the lateral-line bone "Y," often divided into two elements "Y_1" and "Y_2." It is flanked laterally by the operculum. Where "Y_1" and "Y_2" are present, either one contains the lateral extremity of the posterior pit line; the ventral surface of either or both makes contact with the palatoquadrate. Where one "Y" only is present, both these structures can be observed on the posterior half of the bone. It seems impossible to decide in many circumstances if "Y_1" has captured "Y_2" or vice versa. Hence when one bone only is present it is usually simply labelled "Y."

Bone "Z" forms the posterolateral corner of the skull, is loosely articulated, and contains the junction between the main lateral-line canal and the occipital commissure.

Bone "4" (occasionally divided into "4a" and "4b" as in *Soederberghia)* is usually circumorbital, but may be excluded from the orbit as an individual variation (as in certain specimens of *Dipterus valenciennesi).* It is the most dorsally placed element on the infraorbital canal below the element on which the junction between the infraorbital and supraorbital canals takes place. As indicated above this is almost invariably bone "X.'

Bone "3" lies anterior to "4" and forms the upper rim of the orbit. Bones "2" and "1" follow "3" around the orbit, "1" forming its anterior margin.

Bone "O" (sometimes divided) is a nonlateral-line bone lying between "3" and "2" on the outer side and the lateral-line bones on the inner.

Bone "K" lies anteromedial to "X" and lateral to "C." It also carries the supraorbital canal that runs forward from "J."

Bone "L" (sometimes divided) is on the supraorbital lateral-line canal medial to "3" and "O," or medial to "3" and "2" where "O" is not developed. Its posterior edge is in contact with "K," or with "X" when "K" is not developed.

The supraorbital lateral-line bones "M," "N," "P," etc. anterior to "L" vary in number, shape, and position depending on the shape of the snout; it is difficult, if not impossible, to offer definitions of them that are generally applicable. Where "O" is present "M," "N," and "P" can be defined as having contact with it, but even then it is not possible to differentiate between them severally with certainty.

The bones of the cheek are known in detail in only three Paleozoic genera—*Dipterus, Fleurantia,* and *Soederberghia*—in all of which the distance between the orbit and the operculum is much smaller than that between the orbit and the snout. The circumorbital bone "5" (Fig. 4), which is placed below "4," contains the junction between the preopercular (or jugal) and infraorbital lateral-line canals. Bone "8" lies posterior to "5," receives the jugal canal from it, and passes it to bone "9" which forms the posteroventral angle of the cheek. Bones "4," "8" and "9" are in contact with the operculum posteriorly. The infraorbital canal traverses bones "5," "6," "7," and "1" in sequence around the ventral half of the orbit, the latter three bones also forming part of the ventral edge of the skull. The identification of bone "1" is sometimes conjectural.

In addition to the bones defined above there are two others—"T," known in *Dipnorhynchus,* and "H," inferred in *Dipnorhynchus* and *Uranolophus*. It is not proposed to define them until *Dipnorhynchus* is discussed in detail. Full definitions will be found on p. 28.

In a group in which variation is so marked as the Paleozoic dipnoans, it would be naive to suggest that the above definitions will prove applicable in every instance. In particular, the topographic relationships of bones are likely to vary, even within a species, to such an extent that they cannot be recognized by their position alone. However, bones subject to such variations can usually be recognized either by the nontopographical criteria in the definitions, by comparison with normal specimens, or by a process of elimination. Examples are readily to hand in the work of White (1965, fig. 21) on *Dipterus valenciennesi*, one of which is presented in detail here as an illustration (Fig. 4). In this specimen, bones "A," "B," "C," "I," "J," "Z," "5," "8," "4," "3," "2," and "O" can all be recognized by application of these definitions in their entirety. This leaves only the bones White labelled "Y_1," "K," and "L_1," to be accounted for. There is clearly one bone less in this series than in the same position on the standard and most other specimens. The problem is to decide the fate of this bone. The bone labelled "K" satisfies the topographical relationships given in the definition of "K" with respect to "3" and "J," and it receives a lateral-line canal from "J." Apart from the fact that it does not join a normal "X" on its posterior margin it has no peculiarities and is therefore probably correctly identified. The bone labelled "Y_1" then fails to satisfy the definition in that it is

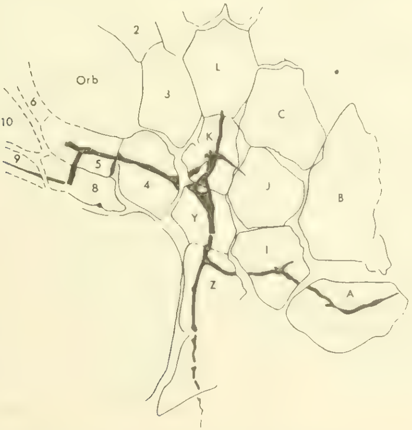


FIG. 4. *Dipterus valenciennesi*. Posterior skull roof and cheek elements, showing lateral-line canals. Redrawn after White (1965) with additional original observations.

bounded in front by "K" rather than "X," it contains the junction of the infraorbital and supraorbital canals, and it adjoins "4." The two latter features are usually characteristic of "X." On the other hand it lies on the lateral-line canal anterior to "X" and is flanked by the operculum and by "I_2," as is normal for a "Y" bone. There are thus three possibilities. The bone White labelled "Y_1" is: 1) an abnormal "X" and "Y" is not present; 2) a fused "X" and "Y;" or 3) an abnormal "Y," and "X" is not present.

There are no signs of two centers of ossification on the bone in question, but it does contain the junction of the infraorbital and main lateral-line canals, a feature associated with "X." It is unlikely to be an abnormal "X" however, for not only would it flank the operculum, but it would also be the only bone available to contact the palatoquadrate. Both of these are characters of "Y" bones. Moreover, the tendency of the canals to focus in a most unusual way on the point of junction of "4," "K," and "Y" suggests an accommodation to the failure of a bone to develop in that position. Such a bone could only be "X." The most reasonable solution therefore is (3), above.

THE SKULL ROOF OF *DIPNORHYNCHUS SUSSMILCHI*

Previous Work

The first major attempt at an analysis of the skull roof of *Dipnorhynchus sussmilchi* was that of Hills (1941). Prior to this, Etheridge (1906) and Hills (1933) had described the external character and arrangement of the bones, but since nothing was known of the lateral-line system the homologies could not be soundly based. The analysis of Hills (1941) has been taken as definitive by all subsequent workers; so far as we are aware no reexamination of the species was attempted until that of Campbell (1965), which was based on a new specimen. The latter involved no reinterpretation of the roof; and the bone nomenclature of Westoll (1949) was used pending more adequate preparation of the specimen. Denison (1968a) has recently reinterpreted the dermal bone homologies of the species on the basis of this latter description and casts of the specimen supplied by us.

In his restoration of 1941 Hills made two major errors—concerning the arrangement of the bones on the occipital region of the skull and the position of the orbit. The posterior part of the roof of the type specimen was not preserved; so he reconstructed it in the light of the known structure of other Devonian dipnoans, particularly *Dipterus* and *Fleurantia*. Unfortunately, this part of *Dipnorhynchus* shows little resemblance to these other genera, as was shown by the discovery of another species, *D. lehmanni* Westoll, in Germany (Westoll, 1949), in which the "lateral extrascapular 1" of Hills was shown to be very much larger than he had suspected.

The occipital commissure of the lateral-line system was not preserved on either *D. sussmilchi* or *D. lehmanni*, but both Hills and Westoll indicated that it passed through the "lateral extrascapular 1" (i.e., bone "I" of Westoll). Our new material shows that the canal does not pass through this bone. Presumably it lay in the bone behind, but this is not preserved. Previous attempts to identify the bones in this region of the skull were therefore doomed to failure.

The second error, which has had more far-reaching effects, developed from a misunderstanding of the relationship of the infraorbital and main lateral-line canals. The canal that Hills interpreted as the infraorbital was not completely excavated; on further preparation it has been found to be a shorter anterior offshoot that does not extend forward onto any other element. In fact the infraorbital canal makes a lateral bend in the bone behind the one containing this anterior offshoot (bone X in Figure 5B) and passes down into the cheek bones. This mistake can be readily understood, for in *Dipterus* the infraorbital canal is given off in the most anterior bone penetrated by the main canal. The incorrect anterior position of the orbits inferred from this information has meant that most bone homologies have been misconceived. This has not been recognized by Denison (1968a, p. 361) who believed that Hills correctly identified "X." The apparently obvious "B" and "C" bones, for example, were interpreted as "B_1" and "B_2" by Westoll (1949) because they were so far back relative to the orbits; and for similar reasons White (1965, p. 26–31) has been led into a new but, we believe, erroneous theory of the early evolution of the rear end of the dipnoan skull.

NEW DATA.

The homologies of the roofing bones of *Dipnorhyncus sussmilchi* will now be discussed using the principles previously enunciated (Figs. 5 and 6). The two avail-

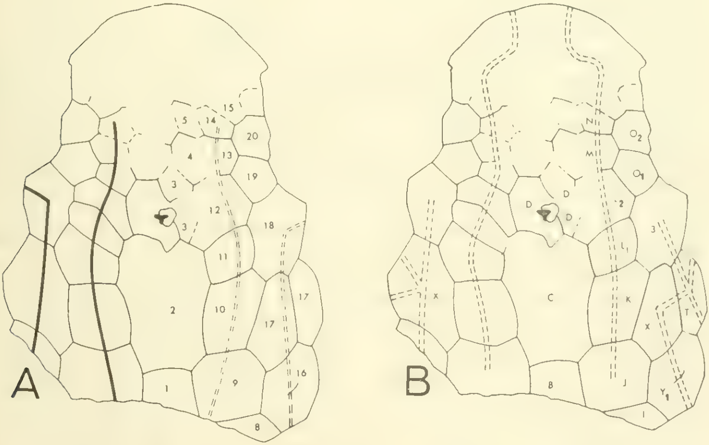


FIG. 5. *Dipnorhynchus sussmilchi*, Holotype. A) Hills' drawing of the skull roof, original notation. B) new reconstruction of the skull roof with new notations. Redrawn from Hills (1941) and original.

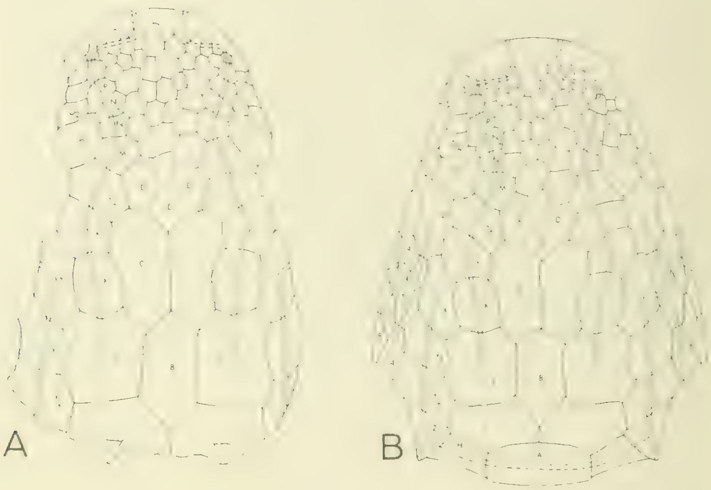


FIG. 6. *Dipnorhynchus sussmilchi*, Specimen 18815. A) drawing of the skull roof. B) reconstruction of the skull in dorsal aspect. After Campbell (1965) and original.

able specimens are different in several features; this necessitates a separate discussion of the bones seriatim.

Bone B and the paired bones C can be readily recognized using the standard definitions, though in one specimen the pairing of the C bones is only incipient.

The bones lying posterolaterally to B and joining along a median suture behind it carry short posterior pit lines that divide at their inner extremities, but do not extend laterally. However, they do *not* carry any part of the occipital commissure of the lateral-line system. On their ventral surfaces they support the dorsolateral cristae that enclose the anterior vertical semicircular canals (see "Braincase"). They satisfy the definition of "I" but are decidedly unusual in their transverse shape and the absence of the occipital commissure. At this juncture they will be tentatively identified as I.

As has been indicated previously (Campbell, 1965) there is a median embayment in the posterior edges of the I bones of specimen 18815. On preparation this excavation was found to have a "stepped" edge that was almost certainly an articulatory surface for a loosely attached bone "A." It is possible to restore this bone approximately from the shape of the contact, as shown on Figure 6B. There is no sign in the newly prepared material of a lateral-line canal passing out of the posterior edge of the I bone; since A normally carries the occipital commissure of the lateral-line canal, it must be concluded that this commissure passed entirely posterior to the fixed I bone. The posterior edge of the skull roof lateral to the contact with A in specimen 18815 is almost completely preserved and shows a sharp cosmine edge surmounting a grooved surface on the bony layer. It is quite dissimilar to the flat, transversely striated sutural surfaces of a fixed roof bone. On the contrary it suggests the presence of loosely articulated bones along its entire length. One of these would be "Z," the bone that in *Dipterus, Fleurantia, Scaumenacia,* and *Sagenodus* carries the junction between the main lateral-line canal and the occipital commissure. Bone Z is small and subtriangular in all these genera, except *Dipterus* in which it is very transverse and in contact with A along its medial edge. As has been already demonstrated, A in *Dipnorhynchus* is relatively small, and if Z were the only element between A and the operculum, it would be an enormous transverse bone, larger than any other in the skull roof. It is unlikely that a loosely articulated bone with such a shape could have existed in this position, since the articulatory edge is arched and movement along an arc of the length postulated would be difficult. It is more likely that there was a smaller lateral Z and another small bone between it and A. This additional bone would be the posterior continuation of the "I" series, and would in fact be the element designated "I_1" that has been postulated in the ancestor of *Dipterus* and observed in *Rhinodipterus secans* by White (for summary see White, 1965, p. 23–26). Having used "I_1" in this way, White designated the fixed "I" bone as "I_2." However, since there is no suggestion that "I_1" and "I_2" ever fuse to form a single "I" element, it would seem to be more reasonable to retain the index "I" for the fixed bone and use "H" for the unattached bone behind it. The symbol "H" is available and is a logical choice, since White used "Z" for the small triangular bone posterior to "Y." Denison (1968a, p. 357–358) has already used it in this sense. Bone "H" would then be defined as an element lying between "Z" and "A" and carrying the occipital commissure of the lateral-line canal. H, A, and Z are not to be considered as forming part of the skull roof proper. Strictly speaking, they are extrascapular elements.

On both specimens "J" is recognized by the standard characters—position with respect to "B" and "I" and the presence of the anterior pit line. It also contains the termination of the supraorbital lateral-line canal as does its homologue in *Dipterus*. It should be noted, however, that the pit line is situated further back on the bone than in other genera, and that it is directed toward a point well behind the midpoint of "B."

The position of the junction of the infraorbital canal with the main lateral-line canal can be determined on each side of both specimens of *D. sussmilchi*, not only from the external pores, but also from the positions of emergence of the canals on the bone margins and from X-ray photographs. It is also quite clear that there is no connection between the main lateral-line canal and the supraorbital canal as there is in *Dipterus*. The arrangement of the canals is shown in Figure 6B. The bone in which the infraorbital and main lateral-line canals meet is large and equidimensional on the left side of the specimen F 10813A. The same space on the right side is occupied by two bones and it is clear that two bones were present in the same position on both sides of specimen 18815, even though on neither side is the outer bone preserved. It is apparent therefore that the left side of specimen F 10813A is atypical, a most unfortunate fact since it was on this side that Hills prepared the lateral-line canals.

In discussing the homologies of the bones in this region, let us begin with the application of the standard definition and assume that, on the three normal sides, the bone in which the infraorbital and main canals join is "X." The infraorbital canal passes out of these bones laterally into a similarly shaped bone where it branches into three. One short branch passes forward into "3," a second downward into what must be another (unpreserved) circumorbital, and a third backward into a cheek bone (unpreserved) lying below "Y_1." What is the identity of this bone where the trifurcation takes place? The only preserved example of it is entirely bordered by sutures; hence it is not a normal "4," though occasional specimens of *Dipterus* in which "4" is excluded from the orbital margin are known (Westoll, 1949, figs. 2F, 3G, 3I). Moreover no other genus is known in which "4" contains a branching canal system of this type. On the other hand, if it is not a "4" it can only be a supernumerary element not known in any other genus. To facilitate discussion let us provisionally label it "T." This would mean that the element lying anteroventral to T must be the circumorbital "4." Support for this view comes from the angle at which the infraorbital canal emerges from "T." The shape of the orbit can be reconstructed from the part of its edge preserved on "3;" the center of radiation of the bone that filled the space between "T" and the orbit can be determined approximately from the angle at which the infraorbital canal enters it. As can be seen from Figure 7A, this bone must have been relatively small and shaped somewhat as shown. Such a bone could not be "5" (as it would have to be if the element labelled "T" were in fact "4"). If it were "5," the cheek bone "8" (see below) would have to fit in the angle between "Y_2," "T," and "5" in order to receive the preopercular canal. It would then also have to receive the canal that runs posterior from "T;" it is clear from X-ray study that it does not. Therefore, the only remaining possibility is that the circumorbital on the lower side of "3" must be "4."

A similar argument can be developed from the left side of the specimen where, despite the fact that the space occupied by "X" and "T" on the right is occupied by a single bone, the infraorbital canal emerges on approximately the same orientation, and the shape of "4" is comparable to that on the left.

Consequently we conclude that the bone labelled "T" on the right side of specimen F 10813A is not the homologue of any bone in *Dipterus,* and we retain the designation "T" for it. On the left side of the same specimen, since there is no sign of two centers of radiation, the single bone in which the canals divide must be either an "X" that has captured the space and canals of "T" or *vice versa.* We can offer no convincing arguments for either possibility.

Posterior to "X," on both sides of specimen 18815 there are two large lateral-line bones. These must be a pair of "Y" elements and are designated "Y_1" and "Y_2" in the order proposed by White (1965, p. 12). No pit lines can be positively identified on them because they are extensively cracked, but there may be a short transverse one on the posterior element on the left side. "Y_2" and the posterior edge of "Y_1" meet the palatoquadrate on their ventral sides.

On the left side of specimen F 10813A only a fragment of the "Y" element posterior to "X" (or "T") remains, but on the right side almost the complete bone is preserved. From the Westoll-lines on this element and the adjacent fragment of "I," it can be demonstrated that there is a "Y_2" element also, though it is probably much smaller than the "Y_1." Unlike the palatoquadrate on specimen 18815, the one here is attached mainly to the posterior part of "Y_1" though it possibly extends back a short distance on the "Y_2." As was shown by Hills (1941, fig. 5), there is a well-defined, medially situated, oblique pit line on "Y_1."

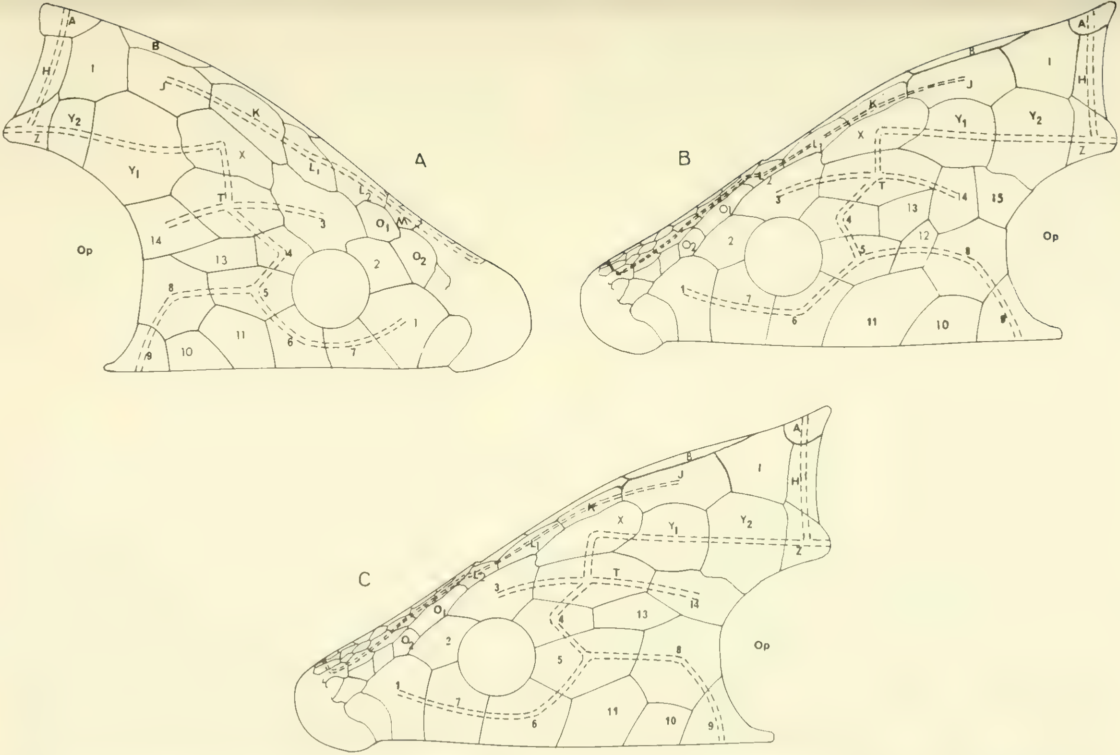


FIG. 7. *Dipnorhynchus sussmilchi*, reconstructions of the cheek. A) holotype, right cheek. B) and C) specimen 18815, alternative reconstructions of the left cheek. Note that in Figures 7B and 7C bone 1 is excluded from the orbit. Bones 6 and 7 could have been made smaller so that 1 could be fitted in at the orbital margin. Had this been done we would have had to insert another bone between 1 and the snout in order to keep its size within reasonable bounds. In the absence of any other evidence to support the presence of such a bone, we have preferred the present reconstructions.

The two specimens differ markedly in the way the "Y" elements are modified to accommodate the operculum. The posterolateral corner of "Y_1" on specimen F 10813A is beveled and presumably the whole lateral edge of the missing "Y_2" must be similar. On specimen 18815 the operculum could not have come so far forward, since only the posterolateral tip of "Y_2" and all of "Y_1" are normally sutured, and delineate the upper outlines of cheek bones.

Once the identity of these bones is established it becomes possible to solve the vexing problem of the homologies of the lateral-line series anterior to "J." In *Dipterus* the first of these bones is "K;" Denison (1968a) has identified it as such in *Dipnorhynchus*. However, in the latter genus it has several peculiar characteristics: it is not in contact with 3; it lies medially rather than anteromedially to "X;" and the distribution of sensory pores on "X" suggests that a cross-commissure of the lateral-line system could develop to the second bone in front of "J." These facts could be interpreted to mean that Denison's "K" in *Dipnorhynchus* is a supernumerary that is lost in all subsequent genera. However, any assessment must take account of the shortening of the cheek and the more posterior position of the orbit with respect to the braincase in *Dipterus*. This backward movement means that "3" and "4" are also further back; consequently "X," "Y_1," and "Y_2" are relatively shorter, and "X" moves back a little with respect to J. Consequently "K" would come to lie anteromedially to "X" and its outer edge would come into contact with "3." From an evolutionary point of view, Denison's identification of "K" is reasonable. The alternative view that his "K" is a supernumerary implies that his "L_1" is really "K." This cannot be substantiated since the bone in question lies in front of the midbrain whereas the standard "K" in *Dipterus* lies opposite it. We therefore support Denison's interpretation.

The homologies of all bones behind a line joining the middle of the orbits have now been established; those of the elements in front of this line present a much more difficult problem. There are two main reference features that can be used with confidence—the circumorbital bone "2," and the pineal stalk. Bone "2" is not preserved on either specimen, but its shape can be inferred with reasonable accuracy from the outline of the orbit on "3," and the sutures on the roofing bones in front of "3." In specimen F 10813A there are two approximately equal equidimensional bones between "2" and the lateral-line series; these are labelled "O_1" and "O_2." A similar pair occurs on the left side of specimen 18815, but on the right side the anterior one is longitudinally divided. The fact that these "O" bones are present is of importance, for "O" occurs in *Dipterus* but not in later genera. Moreover, there are, in both specimens of *D. sussmilchi,* two or three fixed bones anterior to "O_2" lying outside the lateral-line bones. These have no homologues in *Dipterus* in which this region is occupied by the large lateral-line bone "P." There is little point in formally naming them.

The lateral-line bones anterior to "K" are difficult to homologize in terms of the standard nomenclature for *Dipterus*. White (1965, p. 15) uses the convention that "P" in *Dipterus* is the bone where the lateral-line canal turns forward before swinging in toward the snout. There is no reason why this criterion should be applicable in other genera, or indeed why it should be consistent in *Dipterus*. Perhaps a better definition of "P" for that genus would be in terms of its position anterior to "O" and joining the circumorbital "1." As indicated previously, no lateral-line bones are in contact with "1" in *Dipnorhynchus,* but a pair of bones lying anterior and anterolateral to "O_2" and occupying the region of the lateral line just posterior to its medial swing, can be homologized with "P."

"L," "M," and "N" are in contact with "O" on their outer sides; "L" is also in contact with "K" and "C." By using these definitions the "L" bones can be easily identified in both specimens of *D. sussmilchi* except on the right side of specimen 18815 where "L_2" just fails to make contact with "O_1" because of the peculiar shape of the bone in front. Its identity, however, is not in doubt. "M" and "N" are so variable in *Dipterus* and show such a wide range of shapes and invasions that no satisfactory definitions can be developed for them. In *D. sussmilchi* the bones thus named seem to occupy areas comparable with corresponding bones in *Dipterus*.

The lateral-line bones anterior to "P" number four or five on each side of specimen 18815 and probably at least three on each side of specimen F 10813A. They have no homologues in *Dipterus* and are not named here.

The "D" bones of *Dipterus* also show a dismaying variability. If the type skull only is considered, and lip service is paid to the probable, but unproven, hypothesis of the fusion origin of "D," it is reasonable to label the bones grouped round the pineal foramen in *Dipnorhynchus* as "D."

There is no point in attempting to group the median bones anterior to "D" into any scheme. It should be noted, however, that enough of the outlines can be distinguished beneath the cosmine of specimen F 10813A to conclude that there are fewer and larger bones in this region than in specimen 18815.

THE CHEEK OF *DIPNORHYNCHUS SUSSMILCHI*

No cheekbones have been found associated with either of the skull roofs, but in the vacuity of the mandible from Buchan a large lateral-line bone was found to be lodged that we believe is from the cheek of the same specimen. This bone is approximately an equidimensional polygon in shape and is bounded by sutural margins on all sides except one, along which it is beveled. It is traversed by an unbranched angular lateral-line canal the course of which can be traced by X rays and checked from the points of emergence. An array of fine tubules is given off from the main canal on either side of the median angular flexure (Fig. 91B; Fig. 95). A short submedian, arcuate pit line is present. The thickness is uniform except along half the beveled edge and the adjacent edge that contains an end of the lateral-line canals. Toward these two edges the bone is distinctly thicker.

We consider that it can only represent a cheek element, but the alternative possibilities must be briefly considered. Because of the beveled edge on this bone, which indicates a nonsutural margin, the number of possible positions it could occupy is limited to three—that of a "Y" element from the skull roof, a circumorbital, or a posterior cheekbone adjoining the operculum. If it were a "Y," then its orientation could be fixed by the position of the lateral-line canal. When this is done the beveled edge is too far forward for the right side of the skull and too far backward for the left. Further, the inner surface of the bone should show marks of the attachment of the quadrate ramus; though this bone is very well preserved there are no signs of such attachment. If it is a circumorbital, it has to be "4," "5," or possibly "6" since these are the only bones likely to have completely sutured edges apart from the one against the orbit. Of these, "6" can be eliminated because the course of the lateral line would be down rather than along the bone; in any case it has too many sutural boundaries. Bone "5" in *Dipterus* and *Fleurantia,* the only two Paleozoic genera in which it is known, bears the junction between the infraorbital and the preopercular (jugal) canals, but it has no pit line. On both these counts our bone cannot be identified with "5." Finally, "4" can be eliminated because, with the orbit and the suture with "3" fixed by the position of the beveled edge, and the junction with "X" fixed by the lateral-line canal, it can be seen that it could fit only on the left side, and then only if there were a roofing bone between "3" and "X," which is not the case. Also the presence of the pit line argues against its being a "4."

This leaves the hypothesis that it is a posterior cheekbone. If it is one of these, the lateral-line canal in it must be part of the preopercular (jugal) canal, and its orientation is appropriate if it comes from the right cheek. The presence of the pit line on it suggests that it is the homologue of bone "8" of *Dipterus.*

By assuming that the isolated bone "8" belonged to the individual with whose lower jaw it was found, it is possible to scale it down to the size of the available skulls and then fit it into the cheek. The overall dimensions of the cheek can be readily determined since the opercular edge on the Y elements and the opercular articulation on the palatoquadrate fix its posterior, the orbit its anterior, and the palate its ventral limits. It is obvious from these data (Fig. 7) that the cheek of specimen 18815 is proportionally longer than that of specimen F 10813, and that both of them are proportionately very much longer than those of *Dipterus* and later Paleozoic genera.

The difference in the relative sizes of the two cheeks shows that this region must have been variable; therefore bone outlines are unlikely to be stable, and it is possible that the larger cheek may have contained more bones. In these circumstances the outline of bone "8" cannot be regarded as being of vital significance, and alternative reconstructions are possible. Despite this, certain conclusions applicable to both specimens can be reached (Fig. 7):

1) Bone "8" contains no lateral line that could have originated in "T;" therefore there must be one or more bones between them. If it is assumed that "8" is normally heptagonal, there must be at least two. Of these, the element lying in the angle between "Y_1," "T," and "8" will be the one to receive the canal as can be seen from the direction in which the canal emerges from "T." We here designate this element "14." The nonlateral-line bone between "14," "T," "4" and "5" is designated "13."

2) The position and approximate shape of "5" can be fixed from the positions of "4" and the orbit, and from the fact that it must contain the junction between infraorbital and the preopercular canals.

3) At least in the specimen from which our "8" came, there must have been two bones ventral to it because of its shape and sutural characters. The posterior one would have been the homologue of "9" in *Dipterus,* since it would have carried the extension of the preopercular canal. This relatively small bone would be articulated with the palatoquadrate just above the jaw articulation and would therefore be somewhat thickened. This is in agreement with the thickening of our example of "8" in the corresponding direction. Presumably the anterior one would have been the homologue of "10."

Given these conclusions it becomes possible to discuss differences between the two specimens. In specimen F 10813, the inferred sizes of bones "8" and "5" suggest that they are in contact. If this is so, there is likely to be another bone ventral to both of them and anterior to "10." This could appropriately be designated "11" (see Fig. 7A). The shape of this bone, and of "6" and "7" that lie anterior to it, are entirely conjectural. However, there is good control on the shapes of "2" and "1."

On specimen 18815, the outline of the lower edges of "Y_1" and "Y_2" indicate the slight possibility of the presence of a bone between "14" and the operculum. This we have designated "15" in Figure 7B. Also it is conceivable that "5" and "8" were not in contact, and that there was a small lateral-line-bearing bone "12" between them (see Fig. 7B). The alternative reconstruction shown in Figure 7C is, however, considered to be the more probable.

THE CRANIAL LATERAL-LINE SYSTEM IN *DIPNORHYNCHUS SUSSMILCHI*

Many details of this system have been described in the previous section. It remains only to summarize the most distinctive of these and to complete the description (Figs. 6 and 7). The following features are noteworthy.

1) The occipital commissure must lie wholly on the loosely articulated bones Z-H-A-H-Z.

2) The trifurcation of the canal in T with canals running forward to 3 and backward to 14 is not known on any other dipnoan. However, as noted below, in *Scaumenacia* (Jarvik, 1968) there is a short canal onto 3.

3) As has long been known, there is no connection between the supra- and the infraorbital canals; the supraorbital canal extends backward from K to J. These two features are also known from *Uranolophus*.

4) There is no rostral commissure across the dorsal surface of the snout.

5) No junction of the supraorbital canals around the anterior edge of the snout has been demonstrated, though 18815 does show an almost continuous series of large pores around this region.

6) The position of the infraorbital canal has not been observed, but it can be inferred from the data given in the previous section. However, the large pores around the ventral edge of the snout figured by Campbell (1965, pl. 91) and apparently interpreted by Hills (1941, p. 49) as indicating the course of the infraorbital canal, are not connected with a lateral-line canal at all. They, together with the pores mentioned under (5), open into a ramifying set of tubuli occupying the space between the external dermal bones above and the dorsal and anterior wall of the nasal capsule below (see Figs. 69, 71). They are here termed *rostral tubuli*. In addition to opening to the external surface, these tubuli open through one large and numerous small foramina into the nasal capsule. Details of their structure and function are given below. A similar set of *rostral tubuli* occurs in the symphysial region of the lower jaw (see below).

COMPARISON OF *DIPNORHYNCHUS SUSSMILCHI* AND OTHER DIPNOI

Dipnorhynchus lehmanni Westoll. This is the only species, apart from the type, yet assigned to *Dipnorhynchus*. Lehmann and Westoll (1952) interpreted the skull-roofing bones in terms of contemporary understanding of *D. sussmilchi*. The only specimen known does not retain any of the circumorbital bones, and the lateral-line canals are very imperfectly preserved, so that this was the only possible course to follow. Naturally the inadequacies of the interpretation of *D. sussmilchi* were transferred to *D. lehmanni*. Denison (1968a, fig. 3) has offered a new interpretation based on new information; with this we are in agreement, except for the position of the orbits. These he placed too far forward (Fig. 8).

The suggestion of Westoll (*in* Lehmann and Westoll, 1952) that *D. lehmanni* shows evidence of intracranial kinetism finds no support from our interpretation of its skull roof.

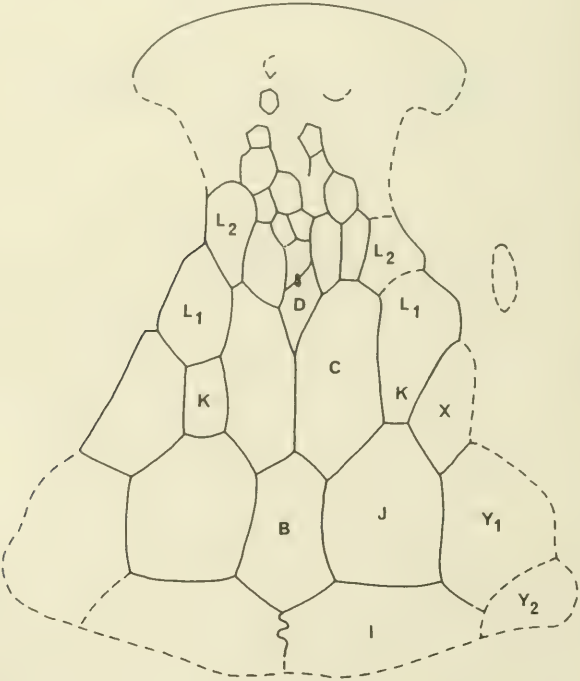


Fig. 8. Skull roof of *Dipnorhynchus lehmanni* modified after Denison (1968b).

The great similarity between the skull roofs of *D. sussmilchi* and *D. lehmanni* is apparent from Denison's figures, and if this alone were considered there would be no grounds for separating them generically. There are, however, considerable differences in the structure of the palates. These are considered in detail below (see Palate).

Uranolophus DENISON. This is the most similar to *Dipnorhynchus* of all the known fossil dipnoans, as is shown by Denison's account (1968a) of the type material from the Lower Devonian of Wyoming (see Fig. 9). The forward position of X and Y_1 with respect to the "eight bones forming a triangular area in the relatively stable posteromedian part of the skull roof" (Denison, 1968a, p. 360), the junction of the I bones behind B, the multitude of small bones in the snout, the absence of a lateral-line canal between bones X and K, and the extension of the supraorbital canal backwards from "K" to "J" are very distinctive features uniting these two genera. *Uranolophus,* however, lacks a pineal foramen, and probably for this reason D is a single stable bone; E is also much larger than any possible homologue in *Dipnorhynchus* and is more like that of *Dipterus.*

The cheek structure of *Uranolophus* has not been described and this is an unfortunate gap in our knowledge. However, Denison's figures 3A, 4, and 5 show enough detail to deduce that the cheek must have been a multiplated complex structure. For example, on his figure 4 the shape of Y_2 and the position of the palatoquadrate (though crushed) show what the shape and position of the operculum would have been; the point of emergence of the infraorbital canal from X

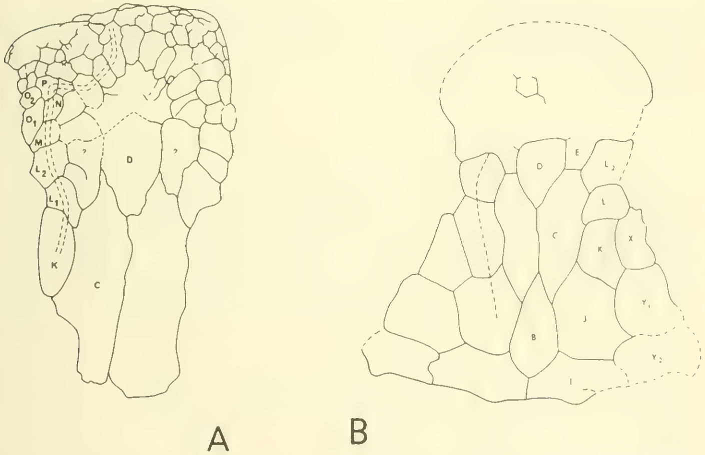


FIG. 9. *Uranolophus wyomingensis.* A) anterior skull roof of specimen PF 3805, Field Museum of Natural History. B) posterior skull roof of specimen PF 1427, Field Museum of Natural History. Redrawn from Denison (1968b).

places the orbit well forward. The outer edges of X, Y_1 imply the existence of two major cheek bones behind 4. On the other hand, the sensory pores on X in figure 5 suggest that the infraorbital canal on that specimen emerged laterally rather than anterolaterally from X, well behind the position of the orbit that can be determined approximately from the position of K. In this case the bone lateral to X receiving the infraorbital canal could not have been a circumorbital and may well have been the homologue of the T of *Dipnorhynchus*.

Dipterus. Further detailed discussion of this genus is unnecessary. Here, for convenience, we summarize the points in which the skull roof of *Dipterus* differs from that of *Dipnorhynchus*. Proportionally the preorbital length in *Dipterus* is much greater; the cheek, the lateral-line series X-Y_1-Y_2, and the non-lateral-line series I-J-K, are relatively shorter; T is completely lost in *Dipterus* and all later genera; the number of bones in the cheek and the length of the cheek are reduced; the bones of the preorbital region are fewer in number and more regular in disposition; the I elements do not meet behind B; H is absent from the extrascapular series; no pineal foramen is present; the bones in the D position are fewer and generally (though not invariably) more regular; O becomes single; the main and the supraorbital lateral-line canals develop a connection between K and X; the lateral-line system on J is reduced to a pit line, which extends on to B; the pit line on I joins with the lateral-line canal on Y_2; the occipital commissure traverses the posterior corner of I rather than passing behind it.

Pentlandia. There are no data on this genus more recent than the account of Watson and Day (1916). The lateral line, the position of the orbits, and the posterolateral corner of the skull are all unknown. However, bone B is readily identified, as also are the paired C and E. The D element has been lost. The lateral-line bones are most reasonably interpreted as in Fig. 10.

Scaumenacia. In general, White's treatment of *Scaumenacia* accords with the principles previously outlined. There are two points of difference between this interpretation (fig. 11) and that of Westoll (1949)—the existence of "K," and the identity of the lateral-line bones adjacent to 2. In all except one of the specimens figured by Westoll (1949, fig. 6) the anterior pit line runs from J to X. This one odd specimen (fig. 6D) apparently has a connection with the plate in front of X on one side, but a normal connection on the other. The unusual side has other peculiar pit line features and can safely be regarded as erratic. We conclude either that the pit line has been captured by X, and K has been lost, or that the plate labelled X by both authors is X + K. The latter alternative can be eliminated since the plate in question is not in contact with C, which is normally developed; moreover, it apparently shows no sign of two centers of ossification. Westoll regards the lateral-line bones anterior to X as the products of a complex set of fusions. The only evidence for his reconstructions is apparently topographical; without other support they must be regarded with caution. White (1965, fig. 36), without comment, goes to the opposite extreme and considers these large bones as single elements. In his single illustration of the genus he labels the element anterior to L_2 as N. In our opinion it is not possible, on the evidence available, to reach a decision on its identity.

Jarvik (1968) has given a restoration of the cheek in *Scaumenacia* showing a short lateral-line canal passing onto 3. This is unknown in any other genus except *Dipnorhynchus.*

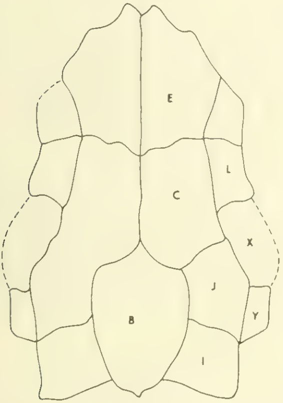


FIG. 10, at left. ***Pentlandia macropterus.*** **Portion of skull roof in dorsal view. Specimen L 10905, Manchester Museum. Redrawn from Watson and Day (1916) with new dermal bone notations.**

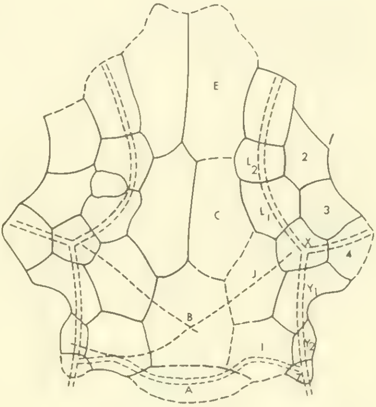


FIG. 11, at right. ***Scaumenacia curta.*** **Portion of skull roof in dorsal view. Unnumbered specimen, Dartmouth College. Redrawn after Westoll (1949) with new dermal bone notations.**

Phaneropleuron. As pointed out by Westoll (1949, p. 147), this genus has much in common with *Scaumenacia.* Our interpretation is given in Figures 12A and 12B. There is no reason to doubt the accuracy of Westoll's identification of bone K, except perhaps in his figure 7E where it may be an X; but without knowledge of the position of the lateral-line canals no decision can be reached on this specimen. The large elements anterior to X or K obviously belong to the *L* series, but we cannot determine if L_1 has captured the space occupied by L_2 in earlier forms, or *vice versa.* They are therefore simply labelled L.

Rhinodipterus. It is probable that two different types have been assigned to this genus, *R. ulrichi* Ørvig (Fig. 13A) from the late Middle Devonian which lacks the bone D, and *R. secans* Gross (Fig. 13B) from the early Late Devonian in which D is well developed. The lateral-line series of *R. ulrichi* is known from the type specimen (Ørvig, 1961, fig. 8); contrary to Ørvig's interpretation it is evident that K has already disappeared. A pit line runs from B through J to X indicating a situation in this region similar to that of *Scaumenacia* rather than that of *Dipterus.* On the other hand. White (1962, figs. 1–2) figures a specimen of *R. secans* in which

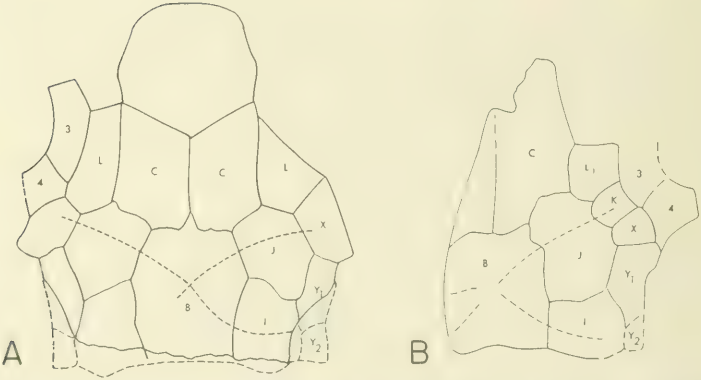

3
L
C
C
L
4
X
J
B
Y_1
I
Y_2
A
C
L_1
3
K
4
X
B
J
Y_1
I
Y_2
B

FIG. 12. *Phaneropleuron andersoni.* Portion of skull roof in dorsal view. A) specimen L 10867, Manchester Museum. B) unnumbered specimen, St. Andrew's University Museum. Redrawn after Westoll (1949) with new dermal bone notations.

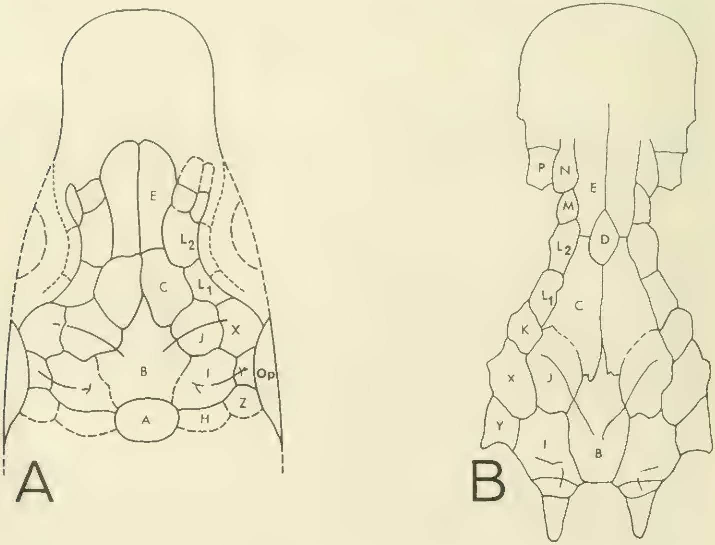

E
L_2
C
L_1
X
J
B
I
Y
Op
Z
A
H
A
P
N
E
M
D
L_2
L_1
C
K
X
J
Y
I
B
B

FIG. 13. A) *Rhinodipterus ulrichi.* Skull roof in dorsal view. Reconstruction. Redrawn from Ørvig (1961) with new dermal bone notation. B) *Rhinodipterus secans.* Skull roof in dorsal view. Specimen P 1451, Institut Royal des Sciences Naturelles de Belgique. Redrawn from White (1962) with new dermal bone notations.

K is almost certainly present. We consider that these two species, as described, cannot be congeneric. The main similarities appear to be the elongate shape of the snout, the paired anterior openings in the snout, and the T-shaped structure of the anterior part of the mandible. The anterior openings are not confined to *Rhinodipterus* but have been found also in *Dipterus*. The other two characters are clearly correlated and probably indicate adaptation to the same feeding habit. The long-snouted *Fleurantia* has a similar mandible structure. These similarities therefore seem to be of less systematic significance than the differences in the skull roof. (Note that for White's reconstruction, O must be present in *R. secans* though it is not preserved, thus confirming the identification of that bone by Gross (1956, fig. 13A). Restudy of the genus *Rhinodipterus* is required.

Soederberghia. This is a most illuminating genus in connection with the fate of K (Fig. 14). In it the supraorbital lateral-line canal from J is still fully developed, as also is the anterior pit line. The supraorbital canal joins the main canal in X at the same point as the infraorbital canal. White (1965, p. 23 and fig. 30) regards this bone as the survivor of 'K' or 'X', probably 'K'," but gives no reason for his preference. Perhaps he was influenced by the forward extension of the bone on the

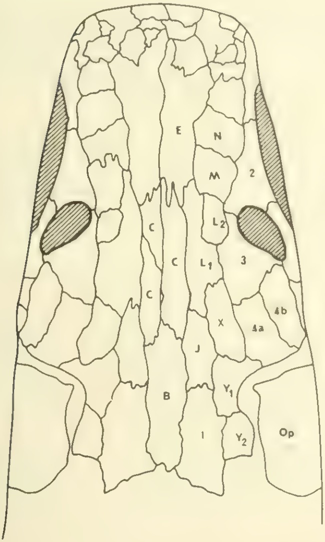


FIG. 14, at left. *Soederberghia groenlandica*. Skull in dorsal view. Reconstruction of the holotype and paratype. Redrawn from Lehman (1959) with new dermal bone notations.

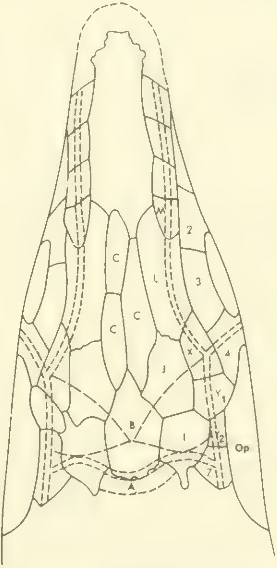


FIG. 15, at right. *Fleurantia denticulata*. Skull in dorsal view. Reconstruction. Redrawn from Graham-Smith and Westoll (1937) with new dermal bone notations.

right side of the specimen shown in Lehman's figure 2 (1959), but that specimen is rather exceptional. Otherwise the bone occupies the normal "K" position, and as the plates of Lehman's work so admirably show, it has a single center of ossification. We regard it as X.

There are two other unusual features of the skull roof of *Soederberghia* that require explanation. In the nomenclature of Lehman (1959), there are two postorbital elements, (the 4A and 4B of our Fig. 14), the upper one of which is not marginal to the orbit. The D bones are very variable, and in different specimens have developed medially, or on the left or right only, or not at all. The M bones also are very erratic. Lehman (1959, p. 20) noted a small plate between the median frontals (i.e., between the two C's), a little behind the orbits. This he referred to as a pineal plate. Occasionally it is missing or a pineal foramen appears to be present. If this structure is properly interpreted it will require a rethinking of the value of relative positions of dermal bones to the anterior elements of the braincase in homological argument. In *Dipnorhynchus*, *Chirodipterus*, and the living dipnoans the pineal organ stands up dorsally from the diencephalon or is directed slightly forward from it. The diencephalon can thus be inferred (or shown) to be below the anterior part of C or the posterior of D. A similar arrangement in *Soederberghia* would place the diencephalon no farther forward than the posterior parts of C. That this could be so is also suggested by the extreme depression of the skull at the level of, and anterior to, the orbits.

Confirmation of this view would render suspect arguments for dermal bone homologies that paid no attention to the anterior shape of the skull roof. There is no reason, however, to question the use of braincase relationships in determining the homologies of the posterior roof elements; in fact, we consider the position of the pineal organ still to be an open question in *Soederberghia*.

Fleurantia. This genus has much in common with *Soederberghia* in addition to its long head. It has lost K, L is very long and extends up lateral to M, and bones D are irregularly developed. We cannot agree with the interpretation of Graham-Smith and Westoll (1937). Our views are represented in Fig. 15.

CARBONIFEROUS AND PERMIAN GENERA. The system of bone nomenclature used above has been developed for Devonian dipnoans. It has long been recognized that the Carboniferous and Permian members of the group have a different structural arrangement on the posterior part of the skull roof. Chief among these differences are the apparent capture of the occipital commissure of the lateral-line system by B and the movement of Z to a more anterior position. If it is possible to show that these apparent changes are real, then it would be necessary to develop a modified set of definitions for these more highly evolved forms. As an example of how this could be done we will now examine *Sagenodus* (Fig. 16). This genus is well known, shows little variation in the skull-roof pattern, has many features in common with other Late Paleozoic genera, and ranges from the Early Carboniferous to the Early Permian. Therefore it can fairly be regarded as representative.

That B has captured the occipital commissure is generally accepted. The element so labelled (Fig. 16) apparently shows no sign of two centers and still retains

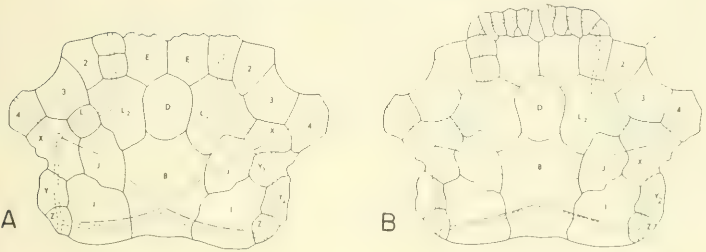
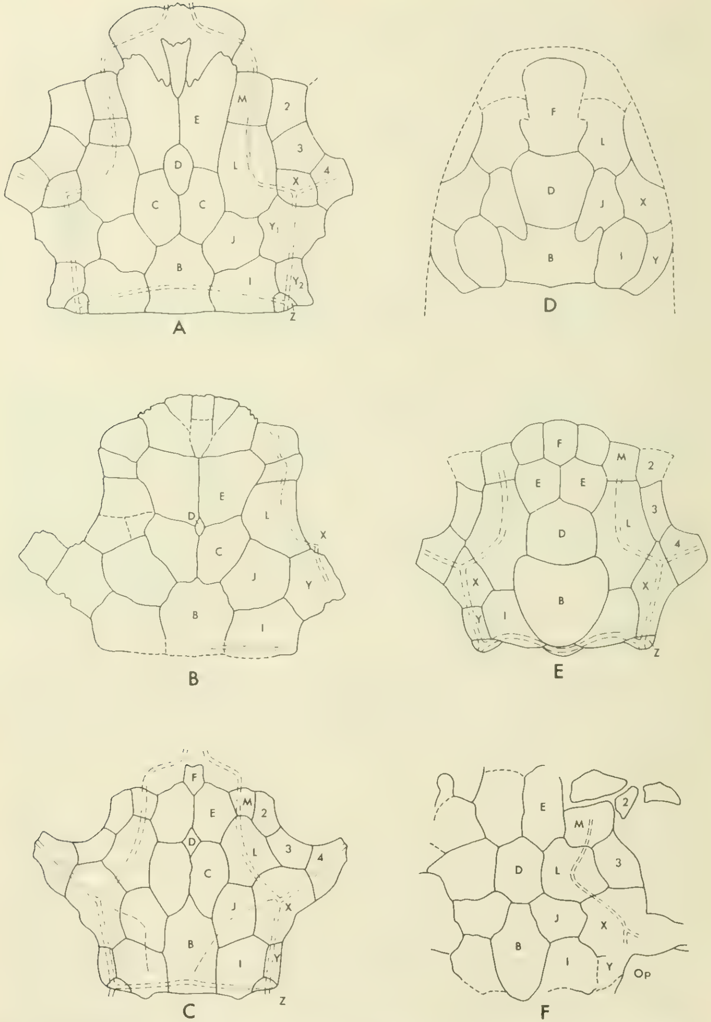


FIG. 16. *Sagenodus*. Skull roof in dorsal view. Reconstructions, showing different conditions of the dermal bone pattern. Redrawn from Westoll (1949) with new dermal bone notations.

both the anterior and posterior pit lines in exactly the same arrangement as the Late Devonian genera *Scaumenacia* and *Fleurantia*. By Late Devonian times the lateral parts of the commissure had already migrated forward from H to I, and it is no surprise to find its median part moved forward to B. Z can still be recognized by the junction in it of the occipital commissure and the main lateral line canal, but it, too, tends to be wedged in between the Y series and I, thus carrying the commissure farther forward. The elements Y_1, Y_2, X, J, 4, and 3, can all be recognized by the same criteria as those for Devonian genera. In Westoll's restoration (1949, fig. 8A-A′) there seems to be evidence from shape (particularly the notch for the articulation of the operculum and the position of the lateral-line canal-anterior pit-line junction), for the fusion of X and Y_1 in some specimens (Fig. 16B). However, Watson and Gill (1923, fig. 1, 2, and 6) show that these bones have a single center of radiation; therefore a more reasonable interpretation is that the space occupied by Y_1 has been captured by X. The fact that X and Y_1 exist independently on one side of some specimens does not affect this argument one way or the other. The position of the palatoquadrate is not known, but we would suspect that, with the incorporation of Z into the fixed series of roof bones, the quadrate ramus would be in contact with Y_2 and Z.

We regard K as absent for reasons given in the discussion on *Scaumenacia*. The bone that lies between J_1 and 3 on the left side of Westoll's figure 8A′ must be L_1 (Fig. 16B). Judging from the radial pattern shown by Watson and Gill on the bones Westoll labels M + L_2 + K, we conclude that L_2 has captured the space that in *Scaumenacia* is occupied by L_1, L_2, and M.

The large median bone in front of B is one of the characteristic features of *Sagenodus*. It lies with its anterior edge at about the mid-length of the orbits and its posterior edge approximately in line with the centers of X: that is, it occupies the normal C space. However, it has a single center of radiation and there is no question of its being due to fusion. In most Late Paleozoic genera in which a pair of C elements is developed, D is very small and does not extend forward beyond a line joining the midpoints of the orbits. Therefore it seems that in *Sagenodus* the median bone D has expanded to capture the space that in other genera is occupied by the paired C and D.


M
2
E
3
D
L
4
X
C
C
Y_1
J
B
I
Y_2
Z
A
F
L
D
J
X
B
I
Y
D
E
D
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C
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2
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FIG. 17. The skull roof in Late Paleozoic and Triassic Dipnoi, all with new dermal bone notations. A) *Ctenodus*. Reconstruction. Redrawn from Westoll (1949). B) *Tranodis castrensis*. Reconstruction. Redrawn from Thomson (1965). C) *Uronemus splendens*. Reconstruction. Redrawn from Westoll (1949). D) *Paraceratodus geramini*. Reconstruction. Redrawn from Lehman (1966). E) *Conchopoma gadiforme*. Reconstruction. Redrawn from Westoll (1949). F) *Straitonia waterstoni*. Specimen 1891.51.4, Royal Scottish Museum, Edinburgh. Redrawn from Thomson (1965).

Therefore, beginning with the definitions developed for Devonian genera, it is possible to work out the homologies of a Late Paleozoic genus with consistency. Only two of the definitions require modification: B does not lie anterior to the bone containing the occipital commissure, and Z is not loosely articulated.

Analyses similar to the one presented above for *Sagenodus* have also been prepared for the other Late Paleozoic genera *Conchopoma, Uronemus, Ctenodus, Straitonia,* and *Tranodis* with consistent results. These are presented in Figure 17.

THE MANDIBLE OF *DIPNORHYNCHUS SUSSMILCHI*

EXTERNAL DERMAL BONES

The external surface (Figs. 18 and 19) is composed of four infradentary bones on each side and a dentary in front. These are well preserved on specimen P 46773 except on the posteromedial surface. The upper surface of the right side of specimen P 33714 also shows fine detail, but on the Buchan specimen (P 13837) the outer dermal bones are much more fragmentary. Nevertheless, the same number and arrangement of bones can be detected.

Perhaps the simplest approach to these bones is through a direct comparison with *Dipterus platycephalus* for which Watson and Day (1916) have provided a nomenclature that is widely applied in its original, or a slightly modified, form (Goodrich, 1930; Westoll, 1949; Lehman, 1966; Denison, 1968a). As will be seen below, there are good reasons for believing that the homologies indicated by this nomenclature are correct. The dentary poses no difficulties. It is a relatively long structure compared with that of other Devonian genera, and on the ventral surface is slightly longer medially than laterally. There is no sign of a median symphysis. Its outer anterior surface is well rounded in general, but it carries a shallow groove that arises posterolaterally from the labial pit (Jarvik, 1964) and runs back along its posterior margin. The upper edge of the dentary extends back along the ramus of the jaw for approximately two-fifths of its total length. Just inside its upper edge there is a

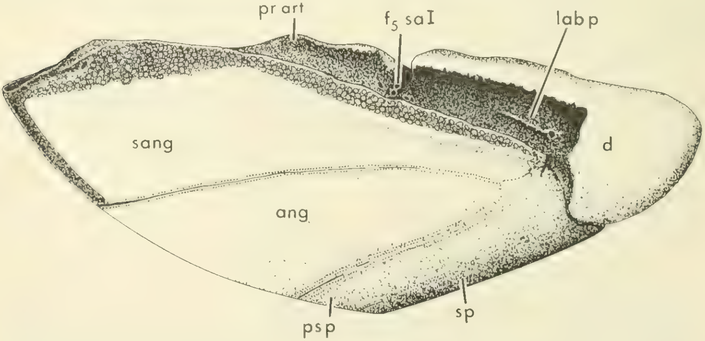


FIG. 18. *Dipnorhynchus sussmilchi,* lower jaw in left lateral view. Based on specimens P 46773 and P 33715, British Museum (Natural History).

shallow furrow that presumably marks its junction with the ossified anterior edge of Meckel's Cartilage. There is a deep incision between the rear edge of the dentary and the prearticular to which it is fused.

The splenials are long, narrow, and subrectangular, the length/width ratio being $^3/_1$ on the P 46773, and approximately $^7/_2$ on the Buchan specimen (P 13837). Their outer edges are slightly arcuate in the Buchan specimen; the width of the bones increases toward the front, where they are in contact with the dentary only.

The postsplenials are longer but have about the same length/width ratios as the splenials. Their outer edges form an outwardly convex arc. Along their anterior edges they are in contact with the dentary, and for a short distance anterolaterally they touch the extremity of the surangular as is shown in Figure 18.

The angular has the outline of a slightly distorted triangle with an obtuse posterior angle against the postsplenial measuring 100°–110°, and the two remaining angles approximately equal. The surface of this bone bulges slightly on both specimens, so that it stands out clearly from its fellows. Its most anterior termination tends to be rounded rather than angular. Both its lateral margins are gently convex outwards.

The surangular has a distorted, elongate, subtriangular outline, but this is modified in various ways. It is greatly produced anteriorly to form a long process that comes in contact with the dentary and the postsplenial; its posterodorsal extremity is truncated to form a relatively straight subhorizontal edge. The whole upper edge of the bone is inflected, the degree of bending being least at the rear, and gradually increasing toward the front of the supra-Meckelian vacuity where it suddenly increases to make the junction with the Meckelian bone underlying the prearticular. This sharper inflection is produced by bending that is almost angular rather than arcuate so that the labial pit, which is in part floored by this surface of the surangular, tends to have a subangular outer edge. The smooth line along the posterior edge of the infradentaries is broken at the junction between the angular and the surangular, the edge of the surangular being set slightly, but distinctly, forward of the general alignment. The whole upper surface of the surangular is covered with small well-rounded beads that are quite densely packed. These seem to have the same structure as the similarly shaped tubercles on the body scales.

On the specimen P 46773, the margins of the separate elements are completely clear throughout. The surangular, angular and postsplenial are separated by sharply defined sutures posteriorly, but these degenerate into a series of large pores anteriorly. They are flanked on each side by two rows of enlarged pores, which presumably are related to Westoll-lines (Fig. 40). The sutures between the two splenials, and the splenials and postsplenials, are not completely preserved. However, they have no median row of enlarged pores anteriorly, and they are marked by two, rather than four, bordering rows of pores.

On the fragmentary Taemas specimen P 33714, the preserved boundaries between the surangular, the angular and the postsplenial are clearly marked, the sutures in places being quite deep.

The sutures on the Buchan specimen (P 13837) are not sharp, but shallow, rounded depressions are present along all preserved bone boundaries. Part of the boundaries between the two splenials and between the splenials and the postsplenials show enlarged pores over part of their length.

Most of the surface of the infradentaries is covered with shiny, densely porous cosmine, apparently identical with that of the skull roof. However, on the anterior parts of the splenials and postsplenials of both specimens the pores disappear. This could just possibly be due to wear, but more probably it indicates a real change in the character of the bone surface (Figs. 55–62). Mention has already been made of the pores that are apparently associated with Westoll-lines on P 46773. On P 33714, both the angular and the surangular show well-developed normal Westoll-lines. On the surangular the lines that are close to the lower and posterior margins can be traced around on the shiny cosmine surface below the beaded upper surface, indicating the separate nature of the cosmine-covered and beaded surface (Fig. 44; Fig. 80).

On the other hand, the surface of the dentary, which is preserved only on P 46773, is not covered with cosmine but "enamel" (see "Bone Histology"). Though it is smooth and shiny, it lacks the dense mat of fine pores, being perforated only by the numerous pores of the rostral tubuli. Viewed under alcohol the dentine layer of bone shows through as a reticulum of "white matter," infilled with "dark brown matter" (Fig. 57). Individual units of the reticulum are 0.05-0.13 mm in diameter. Along the upper posterior crest of the dentary, where an elongate "tooth" is formed, the dentine has a different character again. It is extremely dense and under alcohol shows a much finer reticulum than the remainder of the dentary surface. The units

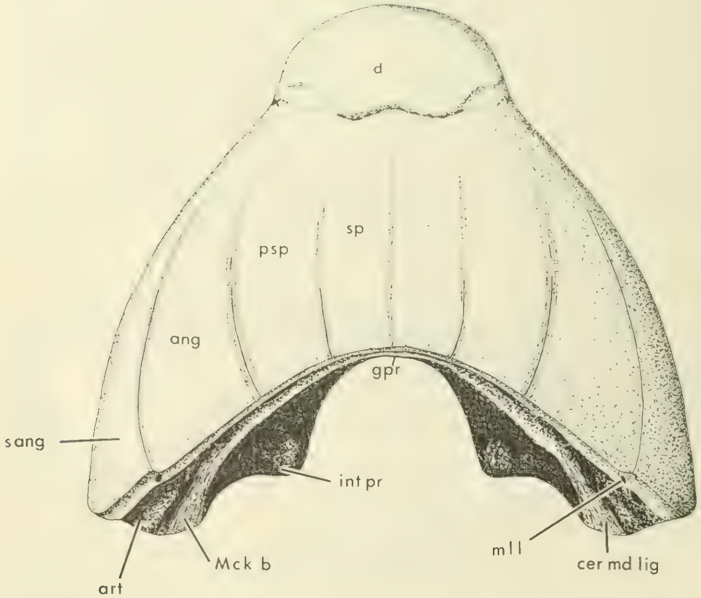


FIG. 19. *Dipnorhynchus sussmilchi.* Lower jaw in ventral view. Same specimens as in Fig. 18.

are 0.03–0.06 mm in diameter. Also, the reticulum is formed of the dark brown matter and the spaces filled with lighter colored matter (Fig. 56). The dentine and enamel surfaces are, in fact, identical with those of the prearticular, a section of which was described and figured by White (1966, p. 7, pl. 1, fig. 1). [Compare also the similar structure on the denticulate edge of the mandible of *Dipterus oervigi* described and figured by Gross (1964).] Along the upper outer edge of the prearticular and dentary, the surface layers are missing and the spongy bone below is exposed (see Figs. 61–62).

THE LATERAL-LINE SYSTEM

The arrangement of the lateral-line canals is clear. They can be traced over most of their courses by natural breaks in the specimens as well as by the positions of the sensory pores. Also specimens P 46773 and P 13837 have been X-rayed, and the canals have shown up with sufficient clarity to enable us to confirm our description.

We have been unable to find a point of exit of the oral canal from the posterior or dorsal margin of the surangular. All available evidence indicates that the canal terminates at, or just behind, the center of radiation of the surangular. There is no posterior connection with any other canal. The oral canal runs forward on the surangular a little above its mid-height, passes along its long anterior process and on to the dentary, though the abundance of relatively large sensory pores in this region suggests that there are probably offshoots into the anterolateral corner of the postsplenial.

The mandibular canal enters the angular in its posterior corner and has a slightly arcuate course on to the postsplenial reaching a point a little posterior to the topographic midpoint of that bone. Here the canal divides into two. The branch forming the mandibular cross-commissure is straight and quite transverse; the anterior branch is also straight, but directed forward so that the two canals lie almost exactly at right angles to each other. Specimen P 46773 is poorly preserved in the region of the medial part of the cross-commissure, but on the right side the branch seems to terminate at the midline of the splenial, though a set of smaller canals radiates anteriorly and anterolaterally from this point. Excavation of a small part of the Buchan specimen (P 13837), however, has shown conclusively that the branches of the cross-commissure do join medially.

The anterior mandibular branch continues forward becoming progressively deeper in the bone (Fig. 52). It passes forward and effects a junction with the oral canal, either just in front of, or behind, the boundary of the "dentary."

On the dentary it has not been possible to demonstrate the course of the canal by X-ray photography. The sensory pores are roughly divisible into two sizes. The larger ones vary considerably in shape from circular to ovate to comma-shaped; they are arranged roughly in two parabolas with their axes directed dorsolaterally (Fig. 40). The upper limbs of the two parabolas meet on the median line, forming a shallow *V*. These do not outline the course of a cross-commissure of the lateral-line canal, as may at first be suspected. They open into the anastomosing rostral tubuli of the symphysial region (see p. 94). The smaller pores are scattered within and lateral to the parabolas and are particularly common around the midline. There are no small pores, however, on the dorsal side of the parabolas.

DERMAL BONES OF THE INNER SURFACE OF THE JAW

The prearticular is a massive bone that dominates the jaw architecture. The dental surface is somewhat differently shaped in the Taemas and Buchan specimens, but the overall similarity is most striking. A rather bulbous prearticular tuberosity (Fig. 20) lies as its anterior extremity opposite the posterior end of the dentary. The tuberosity on the left of the specimen P 46773 is subrounded, but the one on the right is more triangular in outline. On the specimen P 13837 both are much more elongate, and are subrounded in front and taper slightly to the back. Their inner faces opposed the outer faces of the pterygoid elements of the anterior palatal tooth mass, and their posterolateral faces opposed the anterior surface of the lateral tuberosity (see "Palate").

Behind these "teeth" there are the depressions (Fig. 20) that receive the lateral pterygoid tuberosities. Again they are relatively more elongate in the larger than in the smaller specimen, matching the relative shapes and sizes of the adult and juvenile pterygoid tuberosities.

Flanking part of these depressions on each side, and extending posterior to them along the crest of each ramus of the jaw, is an elongated narrow ridge (Fig. 20) that

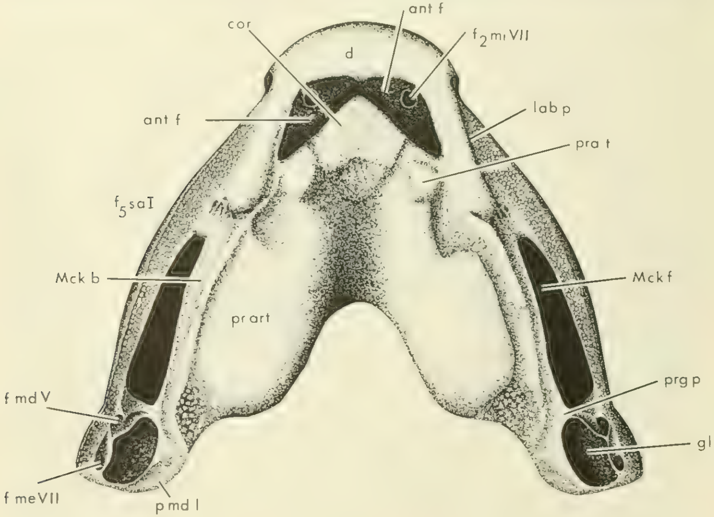


FIG. 20. *Dipnorhynchus sussmilchi.* Lower jaw in dorsal view. Same specimens as in Fig. 18.

forms the dorsal edge of the prearticular. It maintains its height for about three-eighths the length of the supra-Meckelian vacuity, behind which it abruptly loses height and tends to become rather sharper along its crest. It reaches back to a point about three-quarters to seven-eights the length of the vacuity from the front. On the Buchan specimen (P 13837) this ridge is not well preserved on either side, but seems to have had a comparable shape. Inside it on both specimens there is a long lateral furrow (Fig. 20) continuous with the depression receiving the lateral pterygoid tuberosities. It is sharply defined in P 46773 but much less well defined in P 13837. This furrow receives the outer raised edge of the pterygoids when the jaws are shut. The elongate flanking ridge worked against the rather more rounded edge of the pterygoids immediately behind the lateral pterygoid tuberosity.

It is significant that the tubercular lateral surface on the palate of specimen 18815 (Fig. 61) could never have come in contact with this part of the lower jaw, because it is too high up on the palate and around a slight angle.

The inner part of the prearticular forms a large dental surface. It is well and evenly rounded on both Taemas specimens, but is flattened to slightly concave on the one from Buchan, and extends out posteromedially over a subangular prominence (Fig. 19, *int pr*) that gives a very distinctive shape to the jaw. This prominence forms part of the surface of attachment of the very large intermandibularis muscles. The dental surfaces, particularly on the left side, have a subtriangular outline and clearly work against the posteromedian elevations of the pterygoids.

Down the axis of the jaw there is a broad median furrow (Fig. 20) relatively much deeper in the smaller specimen than the larger. This is the median depression of Jarvik (1968), which he interprets as a space for the tongue and for the reception of the basihyal.

All the surfaces of the prearticular mentioned so far are covered with a shiny continuous enamel layer (see previous comment on dentary). A triangular area in the posterodorsal corner of the prearticular, however, has a very rough nodose surface, which is devoid of the enamel layer. This area is rather deeply corroded on the Buchan specimen, but the remnants suggest that it was no different from those on the Taemas specimens, except that it possibly covered a relatively larger area. This surface extends back a little beyond the anterior end of the glenoid fossa and forward beyond the posterior end of the Meckelian vacuity. Its function is not clear.

Posteriorly the dentine shows a rather ragged edge and leaves exposed a large, subvertical, thick wall of "spongy" bone (Fig. 41). In the region of the above-mentioned intermandibular process the bone is 20 mm thick on the Buchan specimen; where it is thinnest it still reaches 7 mm. Along its ventral and lateral edges, this posterior wall of the prearticular forms a tight junction with the thick bar of Meckelian bone previously described.

Forming the anterior part of the interior dermal bones is an element with a triangular anterior outline. This element is probably the representative of the "Md Y" of Jarvik (1967), and the anterior prearticular of Gorizdro-Kulczycka (1950), but might equally be regarded as a fused pair of coronoids. On the Buchan specimen no division between this bone and those behind it can be distinguished, but on P 46773 there is a distinct notched junction at the outer edge and a vague depression toward the midline, producing a rather regular rhombic outline (Fig. 20; Fig. 41). No median suture is visible on either specimen.

Between the coronoids and the dentaries in front is a large deep arc-shaped furrow—the "anterior furrow"—described below. In the Buchan specimen (Fig. 50) the anterior edge of the coronoid is eroded, but it seems probable that it was medially joined with the dentary and formed a thick plate growing out over the Meckelian sheet flooring the anterior furrow and dividing it into two. On the other hand, the anterior furrow is complete in P 46773 (Fig. 41). In it there is only a slight medial projection from the posterior of the dentary toward the acute termination of the coronoid.

The surface of the coronoids meets the anterior pterygoids during mastication, and hence there is complementarity in shape between the two structures. On the large Buchan specimen (P 13837) the coronoids are gently concave overall, but with a slight swelling to the rear. The smaller specimen (P 46773) from Taemas is almost flat anteriorly but quite deeply concave posteriorly.

OSSIFIED ELEMENTS OF MECKEL'S CARTILAGE

The articular is not clearly defined on the Buchan specimen (P 13837), but probably most of it is preserved on the left of P 46773; it is virtually complete on the right of P 33714. Its posterior face, which shows the spongy character of the bone, has a triangular outline and is exposed between the surangular and a bar of dense Meckelian bone. On its upper surface it carries the glenoid fossa, which is approximately 1.4 times as long as it is wide, and shows no sign of being compound (Fig. 20; Figs. 60, 61). The actual articular surface is missing and was, we suspect, formed by a thick cartilagenous pad. In front of the fossa there is a very low, rounded, preglenoid process (partly broken away, Fig. 20) anterior to which the surface of the articular drops away vertically to form the posterior wall of the Meckelian vacuity. The prearticular laps onto the anteromedial corner of the articular.

On the posteromedial side of the glenoid fossa there is a small shelf with the outline of a segment of a circle and with its upper surface striated parallel to its straight edge. It forms the upper face of the bar of dense Meckelian bone referred to above. This shelf lies opposite the similarly shaped and striated surface on the palatoquadrate, and presumably indicates the presence of a palatomandibular ligament. This seems not to have been recorded previously, though in *Neoceratodus* there is a ligament attaching the first visceral arch to the mandible (Greil, 1913, pl. 54, fig. 4). The presence of this ligament in *Dipnorhynchus* cannot be definitely demonstrated, but there are grounds for believing that it may have been present.

In posterior view all specimens show the thick ridge of Meckelian bone lying against the dermal bones and forming the base of the posterior wall of the jaw. This ridge is rather rounded anteromedially, but posterolaterally it broadens and flattens. On the lateral extremity of this flat surface is a slightly differentiated area that may well have supported a ceratohyal-mandibular ligament (see Fig. 19). Much of this flattened surface is delicately striated.

The mesial part of the exposed Meckelian bone on the posterior wall is not only more rounded, as has been mentioned already, but in addition it becomes slightly more prominent. This prominence (Figs. 40, 43; Fig. 53) was probably the site of insertion of the geniocoracoideus muscle. The surface between the intermandibular prominence and the sites of the retractor and geniocoracoideus muscles (Figs. 52, 53) served, no doubt, for the attachment of the intermandibularis muscle. Support for this view can be obtained from the presence in this region of the large foramen that may have contained a branch of the ramus intermandibularis trigeminus that innervates the intermandibularis muscle (see below).

The main ossified element of Meckel's cartilage, which imparts great structural strength to the mandible, forms a thick bar along the inner edge of the supra-Meckelian vacuity and becomes progressively weaker as it extend forward below the posterior end of the dentary. It is this Meckelian bone that would have transmitted the bulk of the stress from the dental surfaces to the articular during mastication. It has a very smooth lateral surface along the median margin of the vacuity where it would have been in contact with the entering adductor mandibulae. On its upper surface, lateral to the ridge on the prearticular (see above and Fig. 20), it carries a shallow furrow that extends back on to the inner side of the articular. In front, this furrow divides into two branches, one extending into the notch between the prearticular and the dentary, and the other into the floor and inner wall of the labial pit (Fig. 40). In this notch there are three or four large foramina, (see below); along the posterior part of the furrow there is a row of similar, but much smaller, nutrient foramina. These demonstrate the presence of soft tissue along the upper surface of the bar, in close contact with the prearticular and the dentary. In the floor of the labial pit there are three more foramina, the most anterior one being in the anterior extremity.

Posteriorly the Meckelian bone rises toward the glenoid fossa where it takes part with the articular in the formation of the low preglenoid process. This process which bears a groove for the mandibularis V nerve (see below) shows no evidence of having been the site of attachment for any part of the adductor muscle.

Lining the medial and anteromedial walls of the Meckelian vacuity is a sheet of Meckelian bone, which thickens considerably toward the mid-line where it fuses with its fellow from the opposite side to produce a powerful vertical symphysical plate. The surfaces forming the medial and posteromedial walls of the vacuity on each side bear a number of more or less vertically arrayed ridges (Figs. 47, 48) which are relatively much more prominent in the Buchan (P 13837) than the Taemas specimen (P 46773). These walls, together with the dorsal wall, also have have numerous impressions of ramifying canals that in places are penetrative. The vertical ridges mark the area of insertion of the adductor mandibulae muscles, and probably of their tendons. This insertion area is extremely large for a dipnoan.

Anteriorly the Meckelian vacuity has a conical termination that extends forward about half the length of the dentary. It is roofed in this region by a thin sheet of Meckelian bone which, in its turn, forms the floor of the very deep arcuate anterior furrow (see above). The Meckelian vacuity is connected to the anterior furrow by a large round perforation (Figs. 20–22; Figs. 46, 50).

The space forward of the Meckelian vacuities and within the curvature of the dentary below the anterior furrow is occupied by a series of coarse, ramifying, bone-sheathed canals (Fig. 54; Fig. 62). These are the mandibular equivalent of the rostral tubuli seen in the snout region and, as previously mentioned, open onto the front of the dentaries at large pores in the enamel surfaces.

FORAMINA AND GROOVES IN THE LOWER JAW

In the following paragraphs we present an account of the various foramina and grooves that mark the bones of the lower jaw in *Dipnorhynchus sussmilchi* (Figs. 21, 22). There are several reasons for making a separate description of these features. They pass between and among different elements of the jaw and are more easily described together rather than piecemeal. Also, the identification of these grooves has been difficult but, we believe, is made easier when the whole vascular and nervous system is considered together. Comparative information on foramina and grooves in the mandibles of other fossil dipnoans is almost wholly lacking (see below, "Comparison"), and therefore we have had to rely almost exclusively upon descriptions of the anatomy of *Neoceratodus* (Greil, 1913; Bertmar, 1959; Fox, 1965) as a guide to the identification of the fossil structures. As will be seen, in large part it is possible to make close comparisons between the nervous and vascular systems of *Neoceratodus* and *Dipnorhynchus*. The reader is advised, however, that these comparisons are wholly provisional. For this reason we have been careful to separate observation from interpretation in the following text.

Lateral and anterolateral to the glenoid fossa there are three foramina that pass vertically downwards into a short wide canal leading into a large chamber (Fig. 21, *ch*) in the outer part of the articular. The largest of these external foramina, or the canal associated with it, is clearly preserved on all three specimens. The other two are definitely distinguishable only on specimen P 33714 from Taemas, although they can be detected on the other specimens with difficulty. The anterior and middle foramina (Fig. 21, *ff md V*) are considered to have carried the mandibular ramus of the fifth nerve which presumably, as in *Neoceratodus* (Fox, 1965) passed downward from the braincase lateral to the masseter muscle giving off several small branches just dorsal to Meckel's cartilage. In *Dipnorhynchus* its passage onto the jaw is marked by a groove across the preglenoid process. Probably, as in *Neoceratodus,* this nerve divided into two main parts, an anterior ramus mentalis V and a posterior ramus intermandibularis V. We consider a groove (Fig. 21, *gr mV + VII)* leading forward from the large chamber in the articular (seen in P 13837) to have carried the r. mentalis V forward on the inner side of the surangular in the wall of the Meckelian cavity.

The third dorsal foramen *(f me VII)* leading into this region is in the correct position to receive the ramus mentalis externus VII (see below, "Braincase"); this probably branched within the mandible along with the ramus mentalis V. It is suspected that it may have continued forward to some of the rostral tubuli, but this cannot be demonstrated.

Leading directly backward from the common chamber in the articular is a broad canal emerging on the posterior face of the mandible between Meckel's cartilage and the margin of the surangular at a large foramen (Figs. 21, 22, *f int V*). This foramen shows evidence for the passage of three elements (Figs. 51, 52). A large posteroventral embayment in the foramen passes into a groove that runs ventrally down the junction between the Meckelian bone and the surangular and angular; a smaller posterodorsal embayment runs posteriorly. These probably carried the anterior and posterior branches of the ramus intermandibularis V that had branched off from the ramus mandibularis V within the chamber in the articular bone. A still smaller dorsal groove within this common foramen runs along a shallow furrow between the articular and surangular and then off the mandible lateral to the glenoid fossa. Its function is unknown.

On the posterior face of the mandible, in the junction between the articular and the posterior band of Meckelian bone, is a foramen (Figs. 21, 22, f_1 *sa I*) with a sharp ventral edge, but with a well-defined furrow in its upper edge (P 46773 and P 33714) or its upper external edge (P 13837). This furrow is continuous with an indefinite groove (Fig. 21, *gr ea I*) that runs along the outer face of the articular just behind the surangular, and then dorsally off the mandible. Internally this foramen opens into a canal that passes between the articular and the posterior band of Meckelian bone to emerge in a large foramen (Fig. 22, f_2 *sa I*), high on the inner lamina of the Meckelian vacuity, immediately below the knobbled surface of the prearticular. These two foramina are interpreted as having carried the superior branch of the first efferent arterial arch. The main arch presumably passes down the back of the mandible. Internally the superior branch runs forward in a distinct groove sending off a strong dorsal branch a short distance in front of the foramen and a ventral branch from a point a little further forward. It then proceeds anteriorly in a broad arc beneath the flat prearticular dental surface. The ventral branch runs along the upper surface of the symphysial septum and enters a foramen (Fig. 21, f_3 *sa I*) in the anteromedial wall of the Meckelian vacuity. From here it is distributed to the canals in the bone below the anterior furrow, some of which are connected with the sensory pores on the dentary. The main canal enters a large foramen (Fig. 21, f_4 *sa I*) situated almost directly below the posterior end of the dentary. From here canals are distributed within the bone to smaller foramina in the posterior ends of the labial pit and the anterior furrow (Fig. 21, ff_5 *sa I* and ff_6 *sa I*). Over most of its course, the groove appears to be double, and it possibly also carried a branch of the seventh nerve. Forward from its posterior dorsal offshoot it gives rise to several tiny, almost imperceptible, grooves that are anterodorsally or anteroventrally directed. From the dorsal branch of the main groove, two very shallow grooves run forward along the bar of Meckelian bone forming the margin of the supra-Meckelian vacuity and enter small foramina in the anterior edge of the vacuity.

The large foramen f_1 ea I is possibly the one labelled *c.ly* by Jarvik (1967, pl. 1, fig. 2) in *Neoceratodus* and interpreted as a lymphatic canal (following Ruge). In P 46773 especially (see Figs. 40, 43) this foramen is entered by two grooves, a broad vague one across the Meckelian bone from the direction of f_1 sa I and a much narrower one along the edge of the dermal bones from f int V. The former probably carried the first efferent branchial artery and the latter a branch of anterior ramus intermandibularis V. It is possible that a branch of the seventh nerve could also enter this foramen. In specimen P 13837 the main groove comes into the dorsal edge of the foramen, but this is probably due to the fact that the artery passed a little further posterodorsally than in the other specimens. From f_1 ea I the artery, and presumably the nerves, are carried forward into the mandible through a short canal and along a groove in the inner surface of the angular and then up into the front of the Meckelian cavity to emerge in one large and several smaller foramina (Figs. 21, 22, ff_2 *ea I*). These serve the complex ramifying system of the rostral tubuli that occupies the space between the thin sheet of Meckelian bone and the dentary, below the anterior furrow.

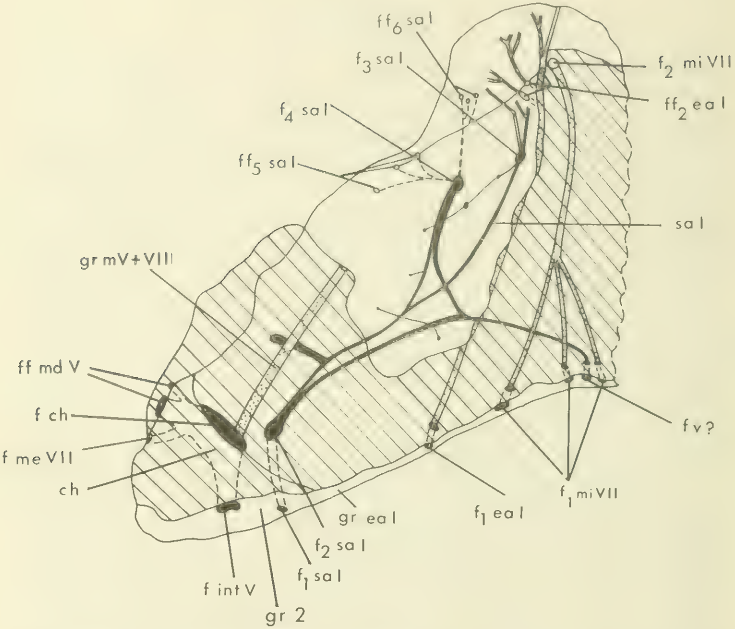


FIG. 21. *Dipnorhynchus sussmilchi.* Ventrolateral aspect of lower jaw. Specimen P 13837, National Museum, Melbourne. Semidiagrammatic representation of vascular and nervous foramina and grooves in the jaw. Solid black indicates structures in or on Meckelian bone, stippling indicates grooves on the inner surface of external dermal bones.

Finally, on both sides of P 13837 there are four small foramina situated on the posterior face of the mandible near the junction between the postsplenial and splenial and the Meckelian bone. (On the left side there are apparently only three foramina on the external surface, but one large foramen apparently provides access for two canals.) In P 46773, a smaller specimen, there are only three foramina in this position on the right side. The same is probably true of the left side though it is too broken to be certain of this. Three of the foramina in P 13837 and two in P 46773 (Fig. 21, f_1 *mi VII*) lead forward through short canals onto grooves uniting on the internal surface of the postsplenial, approximately at its center, and then pass forward as a single groove opening via a large foramen *(f_2 mi VII)* into the anterior furrow. The function of this system is not clear but the foramina are too small to have carried arteries or other vessels. They may well have carried one or more branches of the ramus mentalis internus VII and possibly such a nerve as the ramus alveolaris VII. The fourth foramen in P 13837 and the third in P 46773 (Fig. 21, *fv?*) is larger and is connected to a vertical canal that issues in a foramen

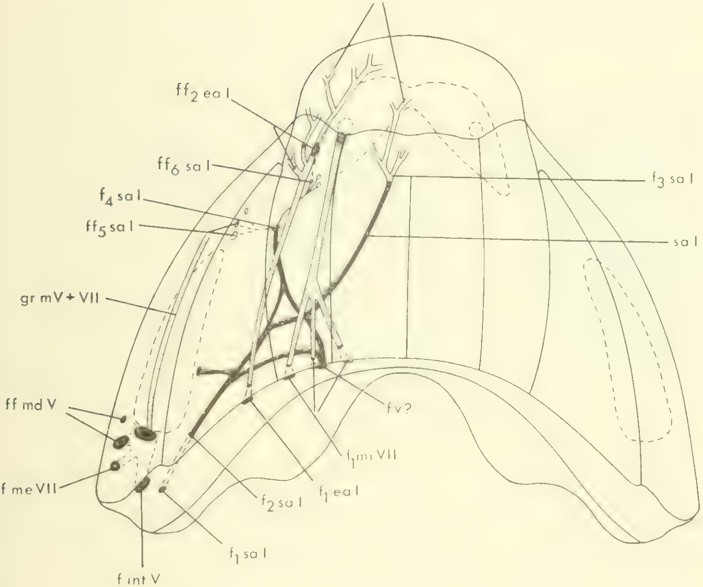


FIG. 22. *Dipnorhynchus sussmilchi.* Attempted reconstruction of the canals, foramina, and grooves for the nervous and vascular systems of the lower jaw.

on the posterior wall of the Meckelian vacuity. This then continues as a groove passing laterally and vertically till the bone begins to arch over to cover the undersurface of the prearticular dental surface. Here it branches. The posterodorsal branch runs back below the previously mentioned groove for the superior branch from the first efferent artery and sends off several short shallow grooves that enter foramina. The anterodorsal branch, which is stronger, crosses the groove for the artery and fifth nerve and then swings anteriorly to run adjacent to the main branch of the same. They enter the bone together (Fig. 21, f_4 *sa l*). From here, as mentioned previously, canals are distributed to the posterior ends of the labial pit and the anterior furrow. This system may have held vascular elements.

We have said nothing of the venous system, but judging from Fox (1965) there is no reason why the lateral venous sinus should not enter the jaw through the Meckelian vacuity and a branch may pass out posteriorly through the chamber *(ch)* and the dorsal notch in the foramen f int V.

COMPARISON WITH OTHER DEVONIAN GENERA

The construction of the mandible of *Dipnorhynchus* is more massive than that of any other known dipnoan. This massive character is achieved by a relative increase of the length of the symphysial region so as to give a greater ventral surface area; but a greater thickness of the Meckelian bone, particularly those parts forming the upper rami of the jaw and the medial symphysis; and by a greater thickness of the dermal bones throughout. Only two other genera have mandibles of comparable shape and strength—the Lower Devonian *Uranolophus* (Denison, 1968a) and the Upper Devonian *Holodus* (Gorizdro-Kulczycka, 1950). However, in neither of these genera is the length of the symphysis relative to the total mandibular length as great as in *Dipnorhynchus*. One would expect to find a correlation between the strength of the jaw and the size of the adductor mandibulae muscles, and hence in the size of the supra-Meckelian vacuity. It is of interest, therefore, to note that in both *Uranolophus* and *Holodus* the supra-Meckelian vacuity is large in comparison with that of *Dipterus* (Jarvik, 1967), but in neither does it reach even half the size of that of *Dipnorhynchus*.

All three of these genera with unusually massive jaws have a specialized nonceratodont dentition, indicating adaptations to peculiar diets. In the case of *Dipnorhynchus* this seems to have been mainly shellfish, and consequently the strength of both bones and muscles is not unexpected. It is clear that though later dipnoans may have had smaller adductor pits, it is not correct to attribute this character to all Devonian genera, particularly the earlier ones (cf. Jarvik, 1967, p. 439).

Melanognathus canadensis JARVIK. This is a recently described dipnoan genus (Jarvik, 1967) concerning which there are problems. Jarvik (1967) gives the age as Lower Devonian but doubt has been thrown upon this by Denison (1968a) who believes it to be possibly no older than Middle Devonian. The main difficulty concerns the structure of the single known specimen—a pair of lower jaws preserved flattened out and showing only the external surface. Because of the potential importance of this specimen we have borrowed and restudied it.

The surface of the dermal bones is covered by a thick shiny cosmine layer such as is often found in Devonian dipnoans and also osteolepid rhipidistians. The cosmine layer bears the openings for the lateral-line organs of the oral and mandibular lines that meet with their fellows of the opposite side in the symphysial region. There is also a cross-connection between the two lines arteriorly on each side. If for the moment we disregard the possible dermal-bone pattern, the arrangement of the lateral lines is quite similar to that in *Dipnorhynchus*.

Jarvik (1967) described the external dermal-bone series in the jaw of *Melanognathus* as being made up of four roughly rectangular bones arranged in a square pattern. A complicated terminology was required for these elements because they seemed so completely different from those of other dipnoans. Jarvik (1967) suggested that this curious pattern in *Melanognathus* was primitive and the one from which all other dipnoan patterns had evolved.

Restudy of the specimen shows, however, that the separations between bones "MdOcl" and "MdMcl" and between these two and "MdOc2" and "MdMc2" are in fact irregular cracks in the cosmine layer. They are not symmetrical on the two jaw rami and there is no evidence of sutures in these positions. The separation between "MdOc2" and "MdMc2," where there has apparently been some slight resorption of the cosmine, is more clear and includes a definite suture. We have been able to find no definite indication of any other suture in the specimen, even by the use of stereoscopic X rays. We therefore cannot at present assign *Melanognathus* to any position of importance in the phylogeny of the dermal bone patterns of Dipnoi. Our safest interpretation of the scanty evidence is that the element "MdOc2" of Jarvik's description probably represents part of the large surangular of *Dipnorhynchus,* while "MdMc2" is the major portion of the angular. (While this study was in progress Dr. H-P Schultze of Göttingen kindly showed us his own re-assessment of *Melanognathus* (now published, 1969) which, though differing in details from ours, is in essential agreement as to the major features of the jaw and the absence of sutures anteriorly defining any "MdOcl" or "MdMcl" elements.)

Uranolophus. Uranolophus shows a pattern of dermal bones basically similar to that of *Dipnorhynchus*, though it seems to be more variable. No definite surangular has been observed, but Denison (personal communication) reports that the surface in the surangular region is not well preserved on any specimen, and this may well account for its apparent absence. Another apparent difference that may be of importance is Denison's record (1968a, p. 378) of "grooves in the cosmine which resemble incomplete sutures" on the ventral symphysial region of one specimen. These grooves "divide this area partially into what appears to be a mosaic of small plates." On the other hand, a *Dipnorhynchus*-like pattern of splenials and postsplenials is shown on the posterior part of the symphysial region of another specimen. It is conceivable that *Uranolophus* indicates the fusion or enlargement of the dermal bones from an ancestral mosaic *after* the separation of the dipnoan and rhipidistian stocks, as was suggested by Denison. However, in view of the tentative nature of the observations, and the similarities between the mandibular bone patterns of *Dipnorhynchus* and primitive Crossopterygii (see "Discussion;" Fig. 24), we remain very dubious of such a conclusion. A further interesting feature in which *Uranolophus* resembles *Dipnorhynchus* is the presence of a deep anterior furrow which is apparently also floored by bone of Meckelian origin (the symphysial plate of Jarvik). No foramina have been observed in this plate, and no rostral tubuli have been noted, though both may well be present. The preglenoid process is short, smooth, and apparently carries a foramen equivalent to the one labelled *f md V* in *Dipnorhynchus,* together with a similar groove that passes inward across its upper surface. Thus, apart from the obvious differences in detention, there is a striking similarity between the mandibles of these two genera.

Dipterus. Because of the significance that has attached to the structures of the jaw of *Dipterus* since the work of Watson and Gill (1923), and the central position given to it in the recent discussion by Jarvik (1967), we have re-examined the two specimens that have become more or less classic, namely L 10858, Manchester Museum, and 53370, Geological Survey, London. In addition, we have prepared another specimen from Caithness (53377, Geological Survey, London). A new reconstruction has been prepared (Fig. 23) and the new specimen is shown in Figs. 63–67.

The anterior parts of all specimens are crushed and it is difficult to be certain of the bone boundaries. However, a median suture and sutures separating splenials from postsplenials can be distinguished posteriorly on L 10858 and 53377. In addition, each of the three specimens is cracked on at least one side in a position that would correspond with the suture between the postsplenial and the angular, while on the right side of 53377 the suture itself can be observed. This, taken in conjunction with the evidence cited by Watson and Gill (1923, p. 208) from a specimen in the Royal Scottish Museum, places the existence of splenials and postsplenials beyond reasonable doubt. The sutures in this region fade away anteriorly, a feature

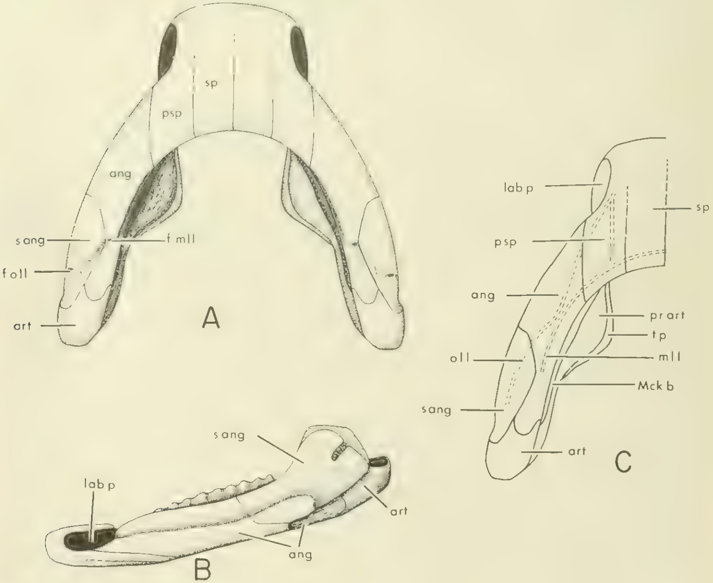


FIG. 23. *Dipterus valenciennesi*, lower jaw. Specimen 53377, Geological Survey, London. A) restoration of the lower jaws in ventral view. B) lower jaw in right lateral view. C) right mandibular ramus in ventral view; diagrammatic, showing the courses of the oral and mandibular lateral-line canals.

that is also shown by the *Dipnorhynchus* material. No suture separating off an element such as the "MdOc1" of Jarvik (1967), and no suture between the dentary and the outer dermal elements behind it, can be observed. The existence in *Dipterus* of "MdOc1" postulated by Jarvik is considered conjectural. The suture between the postsplenial and the angular apparently reaches the edges of the labial pit, but there is no evidence of its position beyond this. Presumably the postsplenial must take some part in the formation of the wall of the labial pit, and if this is so, it is the only part of the splenial or postsplenial without a cosmine cover. The angular ("MdOc2Mc2" of Jarvik) is a large thick bone extending from the labial pit in front to a contact with the articular behind. Its outer surface consists of three parts. The upper (or vertical) portion forms the anterior edge of the supra-Meckelian vacuity and is devoid of cosmine. The median (or horizontal) portion forms an abruptly rounded junction with the upper portion and occupies the major part of the surface. It is cosmine covered and terminates abruptly directly below the deepest part of the adductor pit. Extending back from here along the ventrolateral surface of the articular is the very much smaller third portion. It has no cosmine and must have been deeply buried beneath the skin. The mandibular lateral-line canal must have passed over its surface since it enters the bone in the posterior corner of the cosmine covered median portion, as shown by Jarvik (1967, text-fig. 6A; pl. 5, figs. 1, 4: mc). It is this third portion that Jarvik labels as Meckelian bone (Meck.) on his pl. 5, fig. 1, though he apparently interprets it as dermal bone on all his text figures. A cut through the ramus of 53377 (Fig. 67) shows the angular to be almost triangular in cross section. The bulk of the bone is coarsely spongy, but its inner face is formed of a moderately thick layer of darker colored denser textured bone with very few coarse cavities. It is the posterior extension of this layer that forms the third portion referred to above.

All three specimens show the presence of Jarvik's "MdOc3," the surangular. It is a relatively small element only the anteroventral third of which is cosmine covered. Posteriorly and dorsally the bone covers the outer face of the articular. In its posterodorsal edge there is a notch, probably for the ramus mentalis externus facialis. The oral lateral-line canal enters via a notch in the posterior edge of the cosmine covered surface. The internal structure of this bone is the same as that of the angular.

The lateral-line canals are essentially as they are figured by Jarvik (1967, text-figs. 6A and 7B) so far as we can determine. Unfortunately it has not proved possible to check out their precise course without the destruction of a specimen. However, from the cut in specimen 53377, natural breaks, and the distribution of pores, it has been possible to confirm the position of the whole system except the junction between the mandibular and oral canals on the postsplenial. One feature in which *Dipterus* is different from *Dipnorhynchus* is the depth to which the canals are buried in the bone. In *Dipterus* (Figure 67) they lie almost against the dense inner bone layer and open to the surface through large pores that tend to splay out from the canal. This accounts for the relatively wide scatter of the pores on the bone surface.

Meckelian bone is exposed on the posterior face of the jaw above the inner edge of the angular. It is fragile and crushed on all specimens examined. The prearticular on the other hand is a dense, strong element. Posteriorly it lies against the inner face of the articular as shown in Jarvik's text-figure 6B. Anteriorly it extends for-

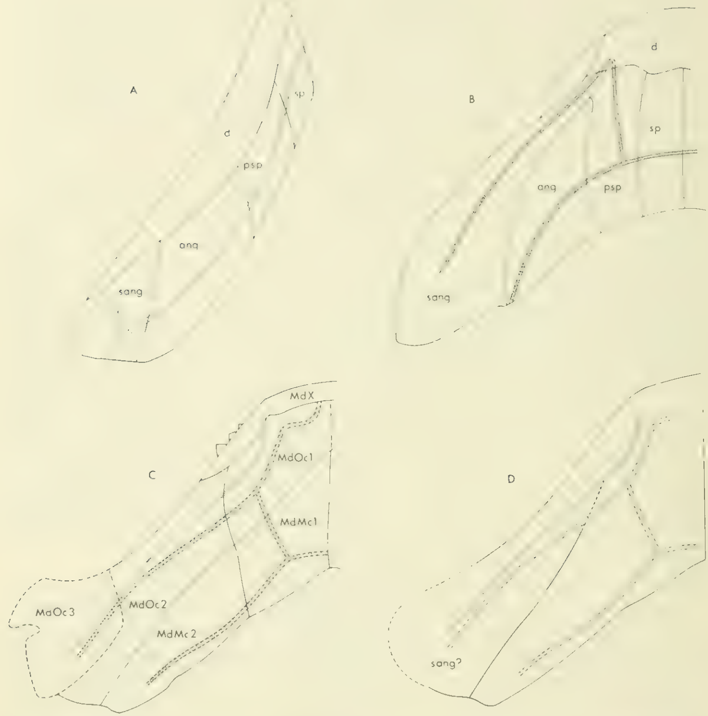
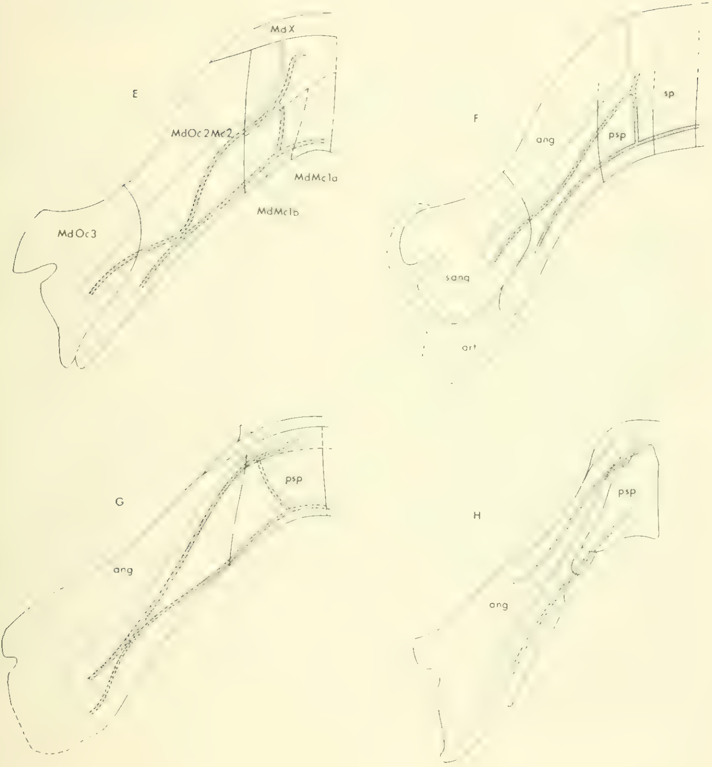


FIG. 24. Dermal bones of the mandible in Rhipidistia and Dipnoi. A) *Holoptychius* (Crossopterygii, Rhipidistia), after Jarvik and various sources. B) *Dipnorhynchus sussmilchi*, original. C) interpretation of *Melanognathus* given by Jarvik (1967), redrawn. D) new interpretation of *Melanognathus*. E) interpretation of *Dipterus* given by Jarvik (1967). Redrawn. F) new interpretation of *Dipterus*. G) *Scaumenacia curta*, redrawn from Jarvik (1967), new interpretation. H) *Neoceratodus*, redrawn from Jarvik (1967), new interpretation. E, F, G, and H appear on p. 61.

ward above the splenial and postsplenial where it unites with its fellow and is supported by the median symphysial wall of Meckelian bones. This region is not well preserved on any specimen, and we find it almost impossible to reconstruct with accuracy. There does, however, seem to have been an anterior furrow in the curve of the dentary, and this must have been floored with thin Meckelian bone. Rostral tubuli may be present in the snout of 53377, but the evidence is not conclusive. There are, however, large pores in the dentary similar to those that open into rostral tubuli in *Dipnorhynchus*.

Apart from obvious differences in detention, the mandible of *Dipterus* differs from that of *Dipnorhynchus* in the following main features. The angular and sur-



angular are relatively much thicker and have a large inflected upper surface devoid of cosmine. We see no reason to believe that the inflected portions are remains of a separate pair of oral canal bones. The surangular is much shorter than in *Dipnorhynchus*, and the oral canal emerges from its posterior edge. This abbreviation of the surangular means that the oral and mandibular canals must be carried forward through the angular; since it is a single bone both canals must be present in the primordia. This, rather than bone fusion or replacement, accounts for the merging of the canals in this bone. Further expansion of the angular at the expense of the surangular, and its final elimination, leads (Fig. 24) to the condition seen in *Scaumenacia* (Jarvik, 1967, text-fig. 5B). The Meckelian bones in *Dipterus* are not nearly so strong as those of *Dipnorhynchus:* stresses were presumably transmitted through the jaw along the thickened outer dermal bones as well as the prearticulars.

In this connection it is important to note that the small Meckelian vacuity permits a strong contact to be made between the prearticular and the angular in front, and both prearticular and surangular are strongly attached to the articular at the rear.

Rhinodipterus. Apart from the highly specialized *Griphognathus*, the only other Devonian genus for which the external dermal bone pattern is reliably known is *Rhinodipterus*. Gross (1956, p. 26–27) and Jarvik (1967, p. 161–165) have described *R. secans* (Gross) in some detail from the single known well-preserved specimen. Though there are obvious differences related to the very large labial pits, there is a clear similarity between this genus and *Dipterus*. This can be well seen from a comparison of our Fig. 23 with Gross' text-fig. 18. The "Infradentale 1" probably contains both splenial and postsplenial elements; "Infradentale 2 and 3" corresponds with the angular and "Infradentale 4" with the surangular. Of particular interest are the lack of cosmine on the upper and posterior surfaces of the angular and surangular, the position of entry of the mandibular canal into the angular, and the foramen for the ramus mentalis externus facialis high on the surangular against the preglenoid process.

Mandibles of the later Paleozoic genera *Sagenodus* and *Ctenodus* are known, but no useful comparison with *Dipnorhynchus* can be made.

We conclude from this survey that the splenial, postsplenial, angular and surangular are primitive dipnoan features; that there is no evidence for fusion of primitive oral and mandibular series of bones; that the transition from the *Dipnorhynchus* type of jaw structure to the *Scaumenacia* type can be readily explained by the progressive elimination of the surangular and the splenial, the space occupied by these bones being captured by the angular and postsplenial (Fig. 24); that the tendency of mandibular and oral canals to run together in the angular in *Dipterus* and *Scaumenacia* can be readily explained by space capture of this type; and that one of the most striking features of the mandibles of the Early and Middle Devonian dipnoans is the essential similarity of their elements of construction despite gross differences in size and shape.

PALATE AND BRAINCASE OF *DIPNORHYNCHUS SUSSMILCHI*

PALATE

DERMAL BONES OF THE PALATE. The ventral aspect of the palate (Fig. 25; Fig. 72; Figs. 74, 75, and 77) shows a pair of partially separate anterior pterygoid elements and posteriorly a complete unbroken bone surface lacking sutures, superficially sculptured into a series of depressions and elevations. A small hypophysial opening is present in the posterior portion of the palate. Specimen P 33699 (Fig. 26; Fig. 73) shows internal and dorsal parts of the palate. In the quadrate region of three specimens (P 33699, 18815 and F 10813) there is a marked shelf behind the posterior edge of the dermal palate, where the ventral surface of the visceral palate is exposed and presumably reveals the separation between dermal and visceral portions.

As shown by P 33699, the dermal part of the palate seems to be formed in two halves, fused in the midline. These must be the principal pterygoid elements, to which separate anterior pterygoids (Fig. 25) are attached anteriorly. There seems to be no indication of the presence of a median parasphenoid element. The pterygoid elements are intimately fused to the visceral portion of the palate. Cross sections of the palate show that the occlusal surface is formed of a layer of dentine (possibly with superficial "enamel") resting on a basal mass of spongy bone. There is no lamellar bone present and the cross sections give no indication of a separation between visceral and dermal units. On the sides of the palate the dentine surface is continued dorsally a short way and then breaks up into a series of small irregular tubercles (Fig. 79). The external surface of these tubercles may be seen, in cross sections, to be continuous with the external surface of the ventral palatal surface and is distinct from the dorsal and lateral surfaces which lack the dentine layer. The tubercular area along the lateral margin of the palate is therefore a region where the dentine layer is interrupted, either through phenomena of growth or (also) because this marks the limit between the skin of the palate and the naked occlusal surface. As we shall later see, the ventrolateral margins of the palate did not form a part of the actual occlusal surface.

The ventral surface of the palate is marked by the previously mentioned depressions, ridges, and elevations which form the only kind of "teeth" in *Dipnorhynchus*. The posterolateral margin of the palate bears a well-marked lateral ridge (Fig. 25, *lr*), separated by an anteroposteriorly directed lateral groove (Fig. 25, *lgr*) from a large posteromedian elevation (Fig. 25, *pmel*) that meets its fellow from the other side in front of the hypophysial opening. The hypophysial opening lies in a shallow, roughly triangular depression formed posteromedially of the two posteromedial elevations just mentioned. Anteriorly, the lateral ridge runs toward a large

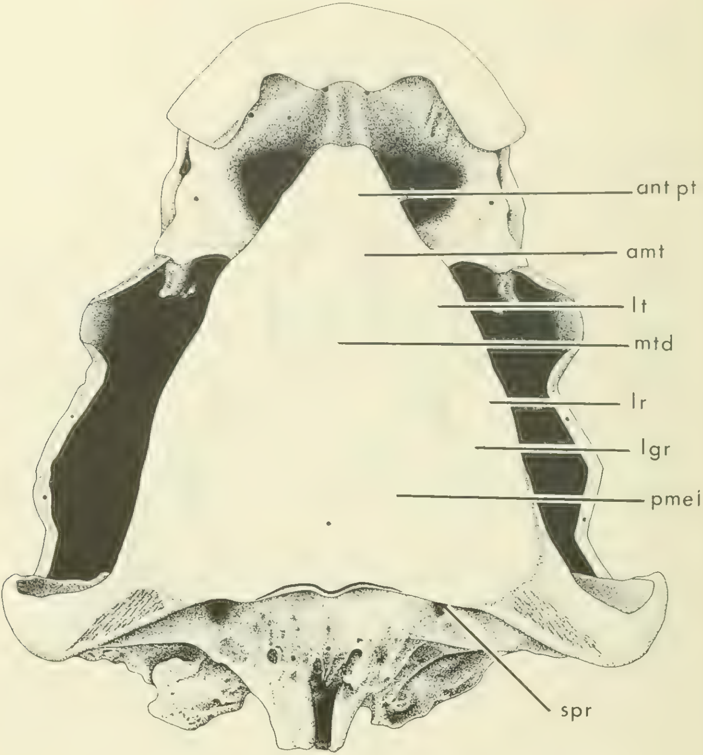


Fig. 25. *Dipnorhynchus sussmilchi.* Palatal view of skull. Holotype.

lateral tuberosity (Fig. 25, *lt*) but is separated from it by a forward extension of the lateral groove that here reaches laterally to the margin of the pterygoid. The lateral tuberosity is very prominent and is anteriorly elongated where it makes a slight bulge in the lateral margin. The lateral tuberosity is partially separated from the large posteromedian elevation by a median extension of the lateral groove that curves round to meet the one from the opposite side in a very shallow transverse depression (Fig. 25, *mtd*). Where the pterygoids meet in the anterior midline there is a large anteromedian tubercle (Fig. 25, *amt)* which fuses with its fellow from the opposite side. This median tuberosity has the appearance of being a single structure in specimen F 10813A, but its paired nature is clearly seen in 18815 and P 33699. The anteromedian tuberosity on each side is located slightly in front of the lateral tubercle and is separated from it by a well-marked deep anterior depression. In specimen P 33699 the anteromedian tuberosity of the right side is considerably larger than that on the left. Presumably this reflects both some abnormality in the occlusal pattern with the mandible and the double nature of the

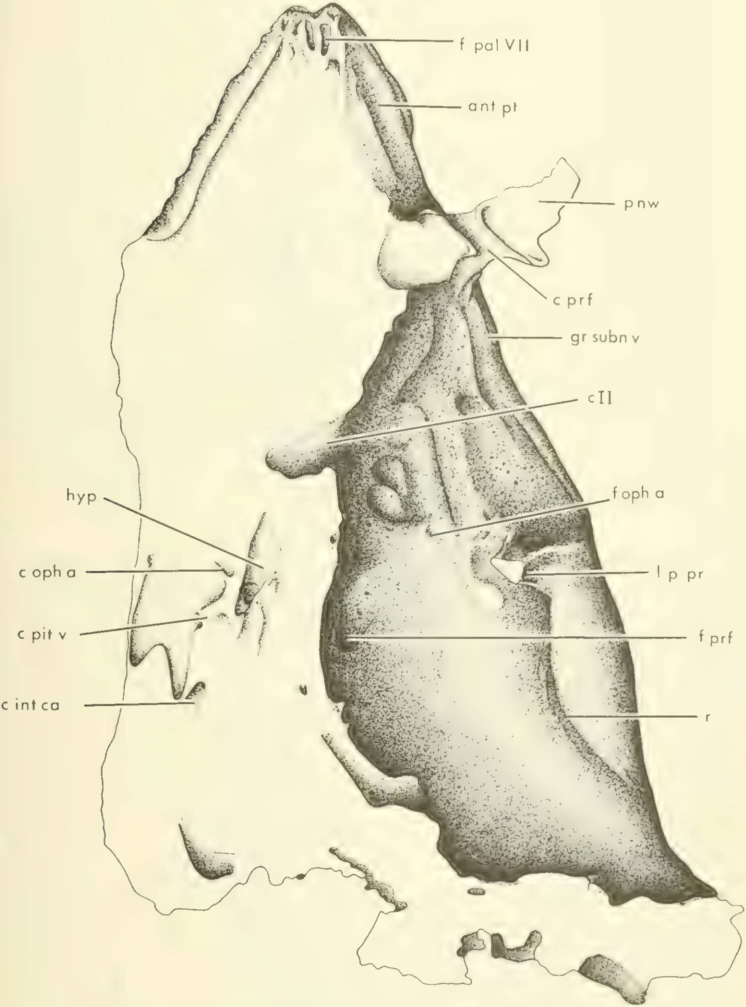

f pal VII
ant pt
pnw
c prf
gr subn v
c II
hyp
f oph a
c oph a
l p pr
c pit v
f prf
c int ca
r

FIG. 26. *Dipnorhynchus sussmilchi*. Dorsal view of detached palate. Specimen P 33699, British Museum (Natural History).

coronoids. In one specimen (18815, Fig. 74) a further anterior tuberosity is present in the midline anterior to the anteromedian tuberosity. This is not present in the other specimens. In specimen P 33699 there is a slight transverse groove in the anterior face of the anteromedian tuberosity that may indicate the coalescence of the two tubercles. The anterior pterygoid (the homology of which is uncertain) has the shape of a narrow strip of bone attached to the anterolateral margin of the pterygoid and reaches in front of the principal pterygoid to meet its fellow from the opposite side. In the largest specimen available (P 33699) there is a triangular space separating the two structures (Fig. 72). This cavity is not present in the other specimens; we presume that in life it was filled with cartilage that for some reason was not calcified in this particular individual. The occlusal surface of the anterior pterygoid is covered with a thin layer of dentine exactly like that of the principal pterygoid. Apart from being gently rounded ventrally it does not form any specially modified dental surface. In specimen P 33699, the occlusal surface of the right anterior pterygoid is flat and on the left side it is very slightly grooved. The functional significance of the variation in shape and curvature of the occlusal surfaces between the three available specimens is not clear. That it is not simply a function of age is demonstrated by the fact that 18815 and F 10813A are of approximately equal size. On the other hand, P 33699 is considerably larger and seems more worn although the dentine layer is apparently intact. There is an interesting problem here with respect to the wear, growth, and replacement of the occlusal surfaces. If separate vomerine elements were present, they are not preserved in the materials studied.

VISCERAL PALATE. The visceral and dermal sections of the palate in *Dipnorhynchus sussmilchi* are fused together in a single mass and, as previously noted, it is difficult to see distinctions between the two portions. It is also difficult to determine the separation between visceral and neurocranial elements in the holostylic skull. However, the optic nerve foramen must be enclosed wholly in neurocranial material, and we may surmise that the separation between visceral and neurocranial elements is at a level ventral to this foramen. Specimen P 33699 is a palate of *Dipnorhynchus* that has become broken away from the neurocranium. As may be seen in Figs. 26, 27, and 73, the specimen includes the ventral margin of the optic nerve foramen and canal and the hypophysial recess, but is morphologically ventral to the endocranial cavity proper. This specimen shows the entire dorsal surface and most other features of the visceral palate.

The line of separation between the visceral palate and neurocranium may be presumed to pass ventrally to the postnasal wall (the ventral portion of which is closely associated with the visceral palate), and the optic nerve foramen. Posteriorly it may be concluded that ascending and otic processes of the palate are incorporated in the side of the braincase (see "Braincase" and "Embryological Analysis"). Ventrally the two halves of the visceral palate are fused in the midline, enclosing the hypophysial recess (Fig. 26), behind which is presumably the morphological position of the basal palatal articulation—here entirely obscured by the complete fusion of palatal and braincase elements. The palate is not continued posterior to the basal region and the posterior margin of the palate forms a distinct vertical "step" in this region.

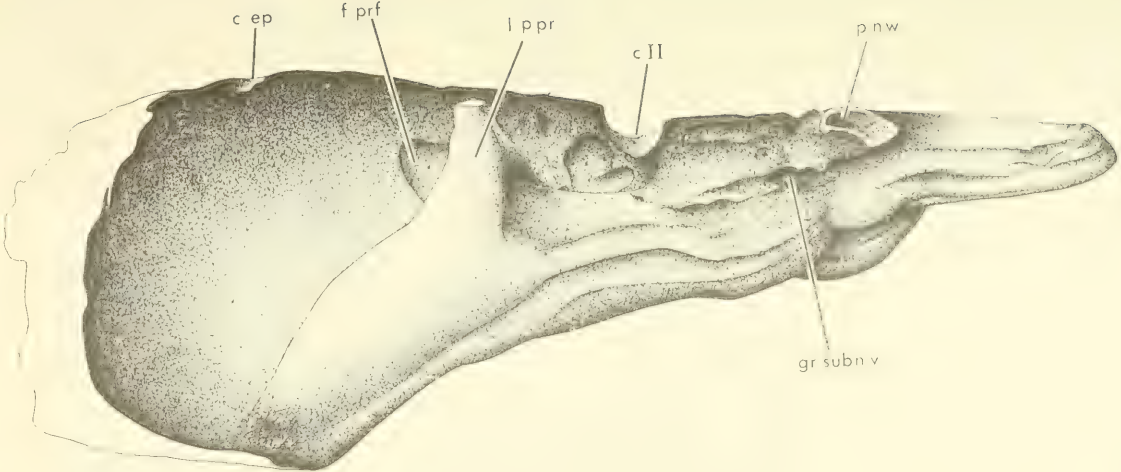

c ep
f prf
l p pr
c II
p n w
gr sub n v

FIG. 27. *Dipnorhynchus sussmilchi.* Right lateral view of detached palate. Same specimen as in Fig. 26.

The visceral palate seems to form two special buttressing regions in the palatal-braincase contact. First, there seems to be a buttress of the palate under the root of the postnasal wall; second, there seems to be a thickening of the visceral palate immediately anterior to the optic nerve foramen (Fig. 26) forming a region of firm palatal-braincase union. A third interesting feature of the visceral palate is a stout conical vertical projection located on the lateral part of the dorsal surface of the palate at a level immediately behind the optic nerve foramen. This "lateral palatal process" (Figs. 26 and 27) seems, in fact, to separate the orbital and temporal chambers of the skull laterally. Its function is obscure. It does not attach to the dermal skull roof nor does it, as far as we can see, form the attachment for any major muscle system. A similar structure is found only in *Uranolophus* among the Dipnoi.

The dorsal surface of the palate posteromedial to the lateral palatal process is an extremely smooth (osseous) surface. This smooth surface extends posterodorsally over the endocranium and forms the floor of the adductor chamber, the extent of which is discussed below ("Braincase"). The floor of the orbital chamber, anterior to the level of the lateral palatal process, is marked by muscle scars, probably for eye muscles (Fig. 26) and a series of foramina for vessels. There is a special concentration of extremely small foramina in a triangular area on the lateral part of the palate, immediately anterior to the lateral palatal process. The internal connections of these various foramina have been determined by radiographic methods. As shown in Fig. 28 and Fig. 94, there is a complicated network of canals for nerves and blood vessels passing through the substance of the palate. A canal for the carotid artery enters the braincase in the otic region and then passes forward to the hypophysial cavity. In specimen P 33699 this canal has a brief connection with the canal for the hyomandibular ramus of the seventh nerve that passes downward through the wall of the braincase from the trigeminofacialis ganglion complex. A narrow canal for the ophthalmic artery (Fig. 28, *c oph a*) passes anterolaterally from the hypophysial recess and opens in the orbital cavity somewhat behind the optic nerve foramen. The distal half of this canal forms a distinct ridge in the dorsal surface of the palate before opening slightly anteromedial to the dorsolateral palatal process (Fig. 26). A larger canal passes almost directly anteriorly from the front of the hypophysial recess. Just in front of the level of the optic nerve foramen this canal divides, one portion continuing directly forward to open in the space between the principal and anterior pterygoids. This canal probably carried a palatal artery. The second branch of the main canal (Fig. 28, *vc*?) turns slightly laterally to run to a point behind the postnasal wall where it opens at four different foramina (Fig. 28; Fig. 94). This second canal is very wide in the material at hand. We do not know what vessel it may have carried. There is also an indication of a wide canal running laterally along the palate just medial of the lateral palatal process. This canal opens at a foramen anteromedial of the lateral palatal process, but again its exact significance cannot be determined. Just in front of the postnasal wall, a large foramen in the lateral margin of the palate leads into a rapidly branching system of minuote canals and probably carried venous elements laterally from the palate. In addition, there is a marked groove along the lateral surface of the palate in the nasal region. This is interpreted as having carried a large subnasal vein posteriorly from the nasal region (see p. 72).

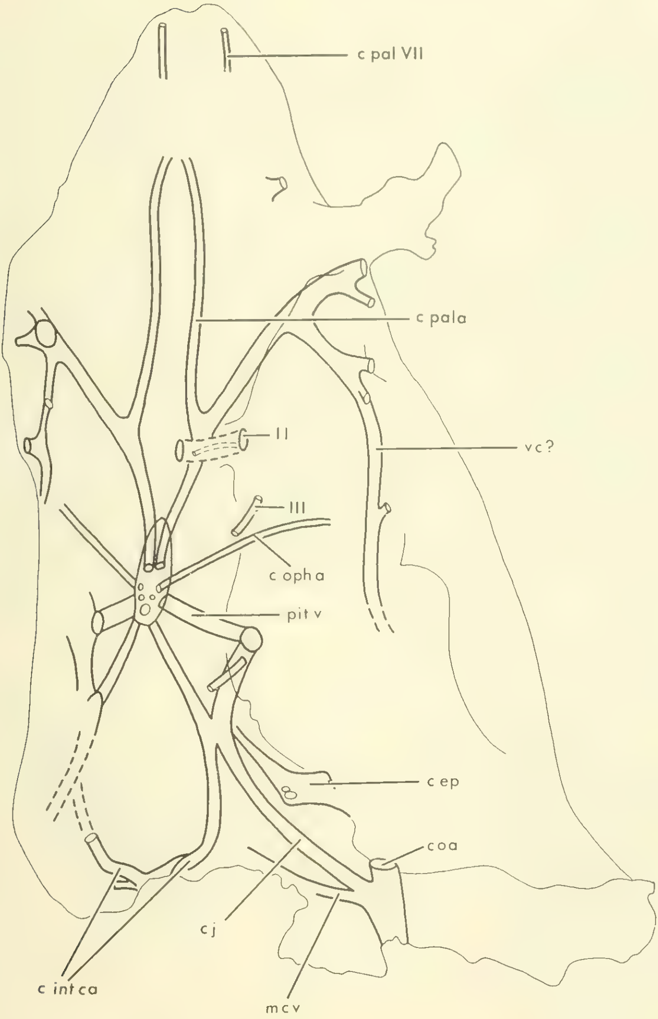

c pal VII
c pala
II
vc?
III
c oph a
pit v
c ep
coa
cj
c int ca
mcv

FIG. 28. *Dipnorhynchus sussmilchi*. Palate in dorsal view showing the courses of various nerve and vascular canals as revealed by direct examination and X-ray photography. Same specimen as in Figs. 26 and 27.

BRAINCASE

As has already been mentioned with respect to the palatal structures, there is considerable difficulty in distinguishing between neurocranial, visceral and dermal elements in the skull of *Dipnorhynchus sussmilchi*. In the following descriptions an arbitrary distinction has been made in most cases. For convenience the braincase will be discussed under four separate headings: nasal, orbital, temporal and otic, and occipital regions.

NASAL REGION. In the material at hand, all portions of the original osseus nasal capsule seem to have been preserved. The floor of the capsule and a ventral part of the internasal septum, if present, were apparently only cartilagenous in life.

There is a complete dorsolateral nasal capsule pierced only by foramina for blood vessels and nerves, as discussed below. Externally, only the dermal covering of the snout may be seen. The "upper lip" curves markedly around the ventrolateral margin of the snout and a short "shelf" of dermal bone thus separates the nasal region from the tip of the snout. The nasal openings are therefore wholly ventrally directed. The space between the dermal bones of the tip of the snout and the anterior perichondral wall of the nasal capsule was apparently occupied by endochondral bone (not preserved) in which the delicate perichondral rostral tubuli ramify. These are shown in Fig. 69. The external openings of these tubuli are seen in the enamel-covered portion of the snout. Internally they connect with the nasal cavity through two large and several very small foramina (Fig. 29, *cc m V*).

A notch in the margin of the bony "upper lip" (Fig. 29) clearly marks the position

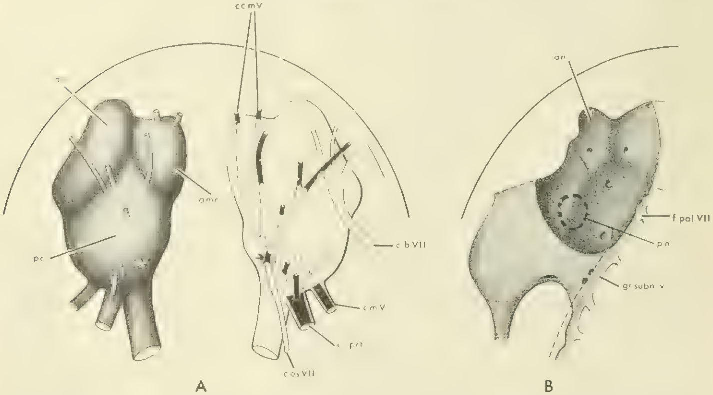


FIG. 29. *Dipnorhynchus sussmilchi*. Reconstructions of snout region. A) reconstruction of the nasal capsule. Left side of drawing shows the shape of the endocranial cavity; right side shows reconstruction of the canals passing through the endocranial cavity and tectum nasi. Portions of canals shown in black are represented by observed canals in specimens. B) nasal chamber in ventral view. Drawn with a portion of the anterolateral margin of the palate removed so as to reveal the groove for the subnasal vein.

of the anterior naris. There is also a small notch in the mid-line (Fig. 75), the significance of which is not clear but which is closely connected with the median internasal septum (p. 88). The position of the posterior naris is not clear. Immediately posterior and slightly lateral to the notch for the anterior naris there is a smaller slightly indistinct notch (Fig. 29B) on the margin of the lip. This does not seem large enough or posterior enough to have contained a narial structure. Immediately posterior to this there is preserved the anterior surface of a larger notch in the upper lip (Fig. 29B). This occurs in many other Dipnoi and such a posterior notch was earlier considered to have contained the posterior naris (see, e. g. Thomson, 1965). However, from the work of Jarvik (1964, on *Dipterus* it now appears that this notch marks the position of a small bony element supporting the fleshy portion of the upper lip. In view of the extremely close similarity between *Dipnorhynchus* and other Dipnoi in this respect (see also Denison, 1968a, b), it is necessary to conclude that the posterior naris was located in a posterior and more medial position, as is shown in Fig. 29B. (This problem is discussed further in our section entitled "Nasal Organ.")

The roof of the nasal capsule (tectum nasi) is thick but consists of extremely cancellous bone with a very thin perichondral layer. The dorsal, external surface is directly applied to the inner surface of the dermal skull roof. The inner surface of the tectum nasi bears three prominent rounded ridges which partially subdivide the nasal chamber into three portions a principal posterior chamber and smaller anteromedial and anterolateral chambers. A series of small canals for the passage of branches of the profundus V and opthalmicus VII nerves (possibly also ophthalmicus V) and also for blood vessels, pass through the tectum nasi opening at small foramina as shown in Fig. 29A. The passage of other small canals, including those opening at these foramina, is revealed by X-ray photographs. The patterns of the canals is shown in Figs. 29 and 30A. The main systems seem to be a series of branching canals, apparently stemming from one main canal, that pass forward in the tectum nasi and then pass ventrally through the tectum into the nasal cavity. These canals probably held the ophthalmicus superficialis VII nerve, which in modern Dipnoi has a similar distribution. Other canals (Fig. 29A) pass dorsally from the nasal chamber through the tectum nasi and these probably held branches of the fifth cranial nerve (Fig. 29A, *c prf*) as well as small blood vessels.

Apart from the small canals and foramina just mentioned, the tectum nasi is complete. Anteriorly and laterally the roof curves ventrally to form the anterior and lateral nasal walls. The anterior nasal wall is pierced by two prominent canals (Fig. 29A) which seem to have carried branches of the fifth nerve and vessels to the rostral tubuli. The lateral nasal wall is moulded around the dorsolateral margin of the anterior narial opening (Fig. 29B). The lateral wall is not continued ventrally to form a solum nasi and, in fact, if such a floor existed it must have been formed only in cartilage, for no trace of it is preserved in the fossils. The lateral nasal wall contains at least one longitudinal canal (as revealed by the X rays) which does not open into the nasal chamber directly and probably carried the r. buccalis VII forward from the orbital chamber (Fig. 29A). The nature of the narial openings will be discussed below ("Nasal Organ").

The internasal septum (septum nasi) is curiously developed. Between the posterior half of the nasal cavities it is dorsoventrally complete and fully separates the principal posterior nasal chambers of the cavities. Further anteriorly, however, the septum nasi is present only as a dorsal band of bone that curves upward as it passes forward and then, at the very tip of the nasal cavity, curves downward again to merge with the anterior nasal wall of each side. The anteromedial nasal chambers of each side are thus not completely separated by the bony septum nasi, although probably in life a ventral cartilaginous extension of the septum had this function. This is a problem of some importance in determining the homology of the nasal septum (see "Embryological Analysis"). As far as we can see no major foramina pierce the sides of the septum nasi.

Posteriorly the septum nasi is completely merged with the anterior portion of the braincase that overlies the palatoquadrate. The triangular tip of the palate projects forward to lie partly under the nasal chambers and presumably in life they were continuous with a cartilaginous solum nasi. Along the lateral margins of the tip of the palate on each side there is a large horizontal longitudinal groove (Fig. 29B, *gr subn v*; Fig. 78) passing backward under the nasal capsule into the orbital cavity. The dorsal rim of this groove was probably continuous with the solum nasi. This groove almost certainly carried a large vein backward from the nasal region toward the suborbital sinus, but there are also several canal openings that probably carried nerves into this groove. The most anterior of these may have served for the exit into the subnasal region of the palatal branch of the facial nerve (Fig. 29B, *f pal VII*).

The canal for the olfactory tract enters the nasal cavity in the posterior part of the internasal septum at a deep recess (Fig. 29A; Fig. 78) just medial to the proximal corner of the postnasal wall. The olfactory tract canal is divided into two portions by a vertical septum.

The principal bony portion of the postnasal wall is a stout ventral bar given off from the anterior portion of the endocranium at approximately the same level as the septum nasi. From a broad proximal base buttressed by the palate this bar extends almost directly laterally behind the nasal cavity. The distal end of the bar is developed into a broadly triangular flange. The anterior wing of this flange

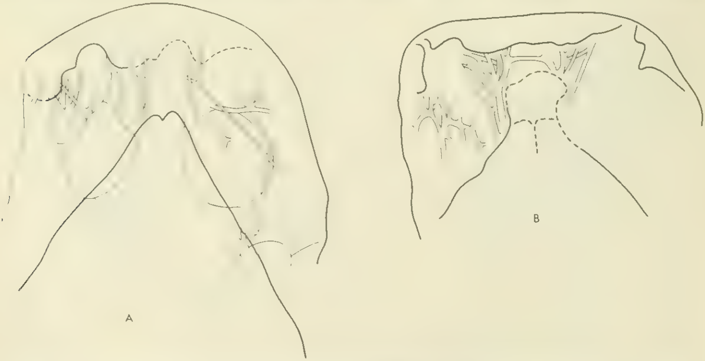


FIG. 30. Drawings showing the outlines of canal passing through the tectum nasi in: A) *Dipnorhynchus sussmilchi* (as shown by X-ray examination) and B) *Dipterus valenciennesi* (specimen 1859.33.612, Royal Scottish Museum).

(Fig. 29B; Figs. 74 and 75) merges with the lateral nasal wall to form the thick posterodorsal corner of the nasal capsule. The posterior wing of the flange reaches dorsally and posteriorly and forms a stout buttress under the inner surfaces of bones "O" of the dermal skull roof and the lateral margin of a deep recess extending forward from the orbital chamber. Dorsally the postnasal wall is continued as a thin lamina of bone that joins the posterior margin of the tectum nasi. This lamina is perforated by a large foramen for the profundus V nerve (Figs. 29A, *c prf*). In one specimen (18815) this profundus canal divides and two foramina—a large ventrolateral one and a small dorsomedial one—are found on the anterior surface of the postnasal wall. Apart from that for the profundus, the only canal to pierce the postnasal wall is fairly wide and opens posteriorly through the ventral surface of the distal part of the wall. This canal (Fig. 29A, *c m V*) is directed dorsomedially and enters the nasal cavity just lateral to the anterior opening of the profundus canal. Possibly it carried a r. maxillaris V or a portion of the profundus lateralis V.

ORBITAL REGION. Details of the external structure of the endocranium in the orbital region are revealed in specimen F 10813A; certain details of the passage of canals through the endocranial wall are revealed in the incomplete specimen P 33699, which has already been shown to indicate a great deal of the structure of the palatal region. From these specimens, and from X-ray photographs of specimen 18815, an almost complete picture has been built up of the structure in the orbital region (Figs. 31, 32). It lacks only detailed information concerning the shape of the endocranial cavity in this region.

The orbital region of the endocranium is here defined somewhat arbitrarily as the portion of the skull posterior to the postnasal wall and anterior to the transverse level of the lateral palatal process. The floor of the orbital chamber is formed

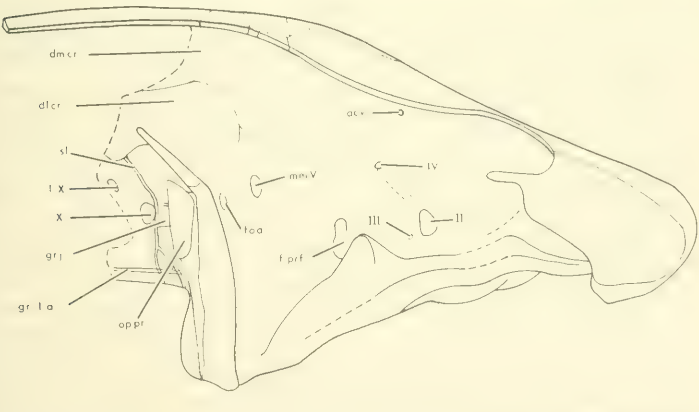


FIG. 31. *Dipnorhynchus sussmilchi*. Holotype. Outline drawing of braincase in right lateral view. Semidiagrammatic.

by the palatoquadrate. The medial wall of the orbital cavity is presumably almost entirely of neurocranial origin.

The following features mark the outer surface of the lateral wall of the braincase in the orbital region. Dorsally, in the deep pocket formed in the medial corner of the postnasal wall there is a foramen for the passage of the r. opthalmicus superficialis VII nerve (Fig. 32, *r os VII*) into the tectum nasi. Posterior to this foramen, just in front of the vertical level of the optic nerve foramen, there are two prominent triangular depressions in the lateral braincase wall. They are believed to be scars from the origin of eye muscles. The optic nerve foramen (Fig. 31; Fig. 78, 81) is large and set in the dorsal part of a depression which is formed by a second series of eye muscle scars. Immediately behind the lateral opening of the optic nerve canal there is a foramen for the third cranial nerve, which passes in a ventral direction through the lateral wall of the braincase before opening at the surface; above it is the foramen for the fourth nerve (Fig. 31, Fig. 73). Ventral and posterior to this foramen there is a laterally directed ridge, formed partly in the floor of the orbital chamber and enclosing the canal for the arteria ophthalmica magna (see above, "Palate"). High on the lateral surface of the endocranium behind the eye muscle scars, there is a foramen which possibly marks the exit of the anterior cerebral vein from the braincase (Fig. 31, acv; Fig. 78).

Even with the use of X-ray photographs, very little of the nature of the endocranial cavity in the orbital region could be determined. The principal distinguishable feature is the large dorsal canal extending upward toward the pineal openings on the skull roof (Fig. 32). It was also seen that the olfactory canals leading forward from the forebrain separate from each other at approximately the transverse level of bones O_1 of the skull roof.

TEMPORAL AND OTIC REGIONS. The temporal and otic regions are here considered together for convenience in discussing the passage of various canals (e. g., for the lateral head vein, hyomandibular nerve, etc.) that pass between the orbitotemporal chamber and the posterolateral face of the otic region.

The temporal region may be considered as bounded anteriorly by the ridge in the floor of the orbital chamber, through which the a. ophthalmica magna passes, and the lateral palatal process. Like the orbital chamber the temporal chamber is roughly triangular in cross section. The palatoquadrate forms its floor, and the neurocranial wall to which parts of the palatoquadrate have become fused (see "Embryological Analysis") forms the medial wall. Posteriorly the great lateral "wings" of the endocranium extend laterally to form the curving posterior wall of the temporal chamber, enclosing the otic capsule in front, and forming a massive buttress for the quadrate-mandibular articulation. This heavy wing of the endocranium is a solid structure and presumably represents the fusion of a processus oticus palatoquadrati with the median neurocranial wall and a massive processus basitrabecularis. The dorsolateral margin becomes narrower and is applied to the undersurface of bone Y_1 or the Y_1–Y_2 contact of the skull roof (Fig. 81). The articular surface (Fig. 77) of the quadrate is not preserved. There is a roughly triangular concave area where the perichondral layer is missing and where we presume that, as on the articular bone of the mandible, there was in life a cartilaginous pad.

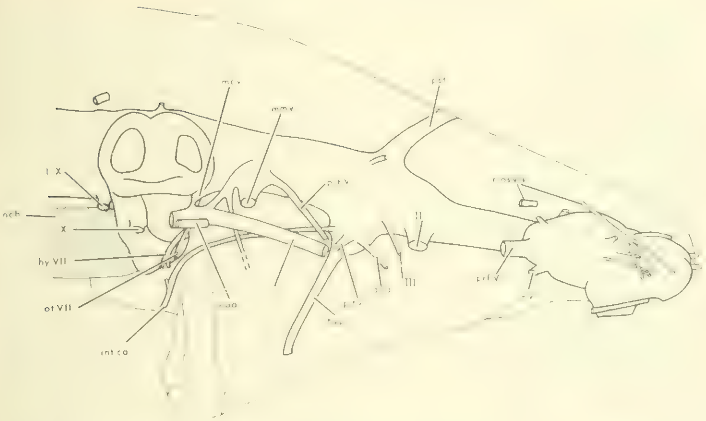


FIG. 32. *Dipnorhynchus sussmilchi*. Reconstruction of the endocranial and notochordal cavities in right lateral view.

The floor of the temporal chamber is an essentially single, smooth surface, marked only by a ridge curving from the tip of the lateral palatal process to the quadrate (Fig. 73). This ridge separates the concave floor of the chamber from a convex anterolateral surface that is a posterior continuation from the orbital region. The anteromedial wall and the ventral part of the posterior wall of the temporal chamber are almost vertical, but the posterior wall is continued posteromedially completely over the whole otic region under dermal bones J and I, giving a very large surface for the origin and enclosure of the temporal musculature. This large posterior chamber is subdivided into two portions on each side by a prominent ridge, the dorsolateral crista, that passes posteriorly and slightly medially, becoming progressively taller until it reaches the undersurface of the dermal skull roof at bone I and the posterior part of bone J. This dorsolateral crista separates a medial recess for the temporalis muscle from a more lateral recess for the masseter muscles. The two medial recesses are separated in the midline by a very thin lamina of bone suspending the endocranium from the underside of the skull roof (Fig. 76). As this dorsal lamina is traced forward, it bifurcates as it comes to contain the parietal stalk passing dorsally from the endocranial cavity.

Anteriorly, slightly behind the level of the lateral palatal process, the median wall of the temporal chamber is pierced by a large anteriorly directed recess marking the opening of the larger jugular canal (Fig. 31, *f prf*). Within it is a small dorsal foramen, which marks the emergence of the profundus nerve canal into the main canal for the jugular vein. Through the medial wall of the recess into which these foramina open is a smaller foramen for the pituitary vein. Directly in front of the anterior limit of the dorsolateral crista is a large foramen (Figs. 78, 81) through which passed the maxillary and mandibular branches of the trigeminal nerve and probably also the ramus ophthalmicus superficialis of the facial nerve.

Immediately lateral to this, facing directly forward, is the foramen for the orbital (stapedial) artery (Fig. 31). The internal connections of these various foramina are discussed below.

As we have already noted, the otic capsule itself is largely obscured by the massive development of the lateral wings of the braincase. The posterior face of the lateral wing of the braincase is very interesting because we may here clearly distinguish, in addition to the neurocranial and palatal elements, a further element that has also become partially fused into this complex (Fig. 31; Figs. 82, 83, 84). This structure is a stout bar of bone that reaches laterally and ventrally across the posterior face of the palatoquadrate. Proximally it is divided and encloses the posterior opening of the jugular canal. It extends laterally as a massive bar, marked by grooves for blood vessels (see below), to a lateral articular facet right at the end of the skull (Fig. 83). This seems to be a facet for the articulation of the operculum. Ventrally, the main portion of the structure continues to the region of the quadrate articulation. The whole structure is separated from the palatoquadrate (except along its dorsal edge) by a deep recess (Fig. 83) that can only be interpreted as a blind spiracular recess having contained a spiracular sense organ (see "Soft Anatomy"). A separate, very narrow, cleft separates the tip of the "opercular process" from the wing of the palatoquadrate. It is tempting to interpret this whole structure as a hyomandibula that has become fused to the palatoquadrate as a structural brace. It has the basic features of a crossopterygian hyomandibula—a double proximal head around the jugular vein, an opercular process and quadrate process (and presumably also a connection, unpreserved, to the ceratohyal). An alternative explanation is that this structure is not a hyomandibula but a massively expanded part of the lateral braincase wall of a type not otherwise seen in fishes and onto which a separate hyomandibula was articulated. However, the facet interpreted here as serving for opercular articulation seems too far lateral in position to receive a hyomandibula. There seems to be no way of resolving these difficulties of interpretation at present. The materials from the Australian Gogo Fauna currently being studied by Drs. Miles and Andrews in Great Britain, may elucidate the problem further.

For the present we will refer to this structure as the "otoquadrate bar."

Running diagonally anteroventrally across the wall of the otic capsule is a narrow ridge enclosing a canal, possibly vascular in origin. Under the projecting wall of the otic capsule is a wide horizontal groove which is the posterior continuation of the jugular foramen and clearly served for the passage of the jugular vein (Fig. 31). A curving ridge on the otoquadrate bar, ventral to the jugular foramen, defines the passage of the orbital artery into the jugular foramen. A second, horizontal ridge on the posterior face of the "opercular process" defines the position of the first efferent arterial arch (Fig. 83). The area immediately ventral to this second ridge seems also to be a region of muscle insertion. The ventrolateral process of the otoquadrate bar is marked by a deep groove for the ramus mandibularis externus VII nerve, running from the spiracular cleft under the otoquadrate bar (Fig. 83).

Within the spiracular cleft are openings for the r. hyomandibularis VII and r. oticus VII nerves. A groove for the ramus mentalis internus VII nerve passes along the posterior face of the lateral wing of the braincase after dividing from the groove for the r. mandibularis externus VII (Fig. 31; Fig. 38).

Further posteriorly, a prominent feature of the otic region is the foramen for the tenth cranial nerve, in the posterior part of the jugular groove (Fig. 32). Immediately ventral to the tenth nerve foramen is a smaller foramen of unknown origin opening into an anterodorsally directed groove. The groove for the orbital artery may be traced ventrally from the jugular foramen towards the groove for the lateral aorta (Fig. 32). Ventrally, the broad base of the otic region between the clefts for the spiracular organs shows a paired structure (Fig. 75). The basal region on each side seems to be continuous with the posterior face of the lateral wing of the endocranium. The only prominent features of this basal region are the presence of a small foramen in the most ventral part of the lateral wall that is connected posteriorly with a groove passing along the ventral surface of the occipital region. The groove (Fig. 31) is interpreted as having carried the lateral aorta, and the foramen as marking the position of entry of the internal carotid artery into the endocranium. Just behind this foramen the groove for the orbital artery curves upward, over the lateral wall of the braincase. One may guess from the arrangement of the otic region that the recesses for the temporalis muscles, between the dorsal and dorsolateral cristae, extended posteriorly over the occipital region under bones A and H of the skull roof. However, the cristae themselves only extended as far backward as the undersurface of bone I. The recess for the masseter muscle, lateral to the dorsolateral crista, terminated over the otic capsule. Since there is no separate region for the insertion of the axial musculature reaching forward from the trunk one must presume that it occupied the posterior part of the "temporalis" recess. Having described the general external features of the temporal and otic region, we may now describe the internal structure. The general shape of the endocranial cavity is shown in Figure 32.

The cavity for the inner ear organ in *Dipnorhynchus sussmilchi* is widely confluent with the general neurocranial cavity. The anterior vertical semicircular canal is distinct and lies within the dorsolateral crista of the otic region. The posterior semicircular canal runs in the posterodorsal margin of the otic capsule; the ridge enclosing it forms the posterior limit of the masseter muscle chamber. The horizontal canal lies just beneath the surface of the otic capsule between the maxillary-mandibular foramen anteromedially and the jugular canal laterally. A vertical septum arising from the posterior wall of the labyrinth cavity separates an anteromedial cavity for the recessus utriculi from a medial recessus sacculi. The latter is confluent medially with the general neurocranial cavity, but is also continued dorsally as the cavity for the crus communis. Anteriorly the lateral wall of the endocranial cavity medial to the trigeminofacialis ganglia is marked by a prominent groove that turns into the anterior portion of the recessus utriculi and then passes out laterally into a canal piercing the lateral wall of the otic capsule and merging into the medial portion of the jugular canal. This is the canal for the vena cerebralis medialis (Fig. 32, *mcv*). No clear indication of the passage of the acoustic nerve is recorded on the bony wall of the capsule. Presumably it left the brain at a point somewhat posterior to the vena cerebralis medialis and passed directly toward the labyrinth organ without touching the bony capsule wall. The floor of the neurocranial cavity is not preserved in the otic region and presumably was a very thin lamina of bone separating the neurocranial cavity from the rapidly tapering notochordal canal (Fig. 32). Anteriorly, at the level of the trigeminofacialis ganglion complex, the floor of the neurocranial cavity bears a prominent long median ridge that may indicate that the myelencephalon in this region had a paired shape. This is most unusual and has not been recorded in other Dipnoi. The notochordal canal, which is wide in the occipital region and the posterior part of the otic region, tapers extremely sharply anteriorly so that it terminates at the level of the midpoint of the recessus sacculi (Fig. 32, *nch).*

The arrangement of the cranial nerves and of certain major blood vessels is largely revealed through study of two important regions: the hypophysial recess and the region of the trigeminofacialis ganglion complex and jugular canal.

The hypophysial recess is best seen in specimen P 33699 (Figs. 26 and 32). A large recess is present, from which an extremely narrow hypophysial canal leads ventrally to the hypophysial opening in the palate (Figs. 26, 32, *hyp;* Figs. 74–75). Leading out of the recess on each side are three major canals. The posterior one (Fig. 32, *int ca*) may be traced backward into the occipital region; it is the canal for the internal carotid artery. This leads through the base of the otic and temporal region, very briefly enters the jugular canal near its connection with the profundus canal, and then bends medially to enter the hypophysial recess. The middle canal opening into the hypophysial recess on each side leads directly laterally and opens into the anterodorsal portion of the recess at which the combined profundus-jugular canal opens into the temporal chamber. This is the canal for the pituitary vein (Fig. 26, *c pit v*). The anterior canal passes anterolaterally to open into the palate just lateral of the optic nerve foramen. This is the previously mentioned canal for the arteria ophthalmica magna which presumably branches from the internal carotid artery within the hypophysial recess.

The jugular vein (or lateral head vein) runs posteriorly through the otic region in a wide canal, the anterior opening of which is in the temporal chamber and also serves for the exit of the profundus V nerve into the temporal region. It opens posteriorly at the jugular foramen as previously discussed. The orbital artery also passes into the jugular foramen and then branches off and opens anteriorly through a separate canal and foramen (Fig. 31, *f o a)* into the temporal chamber.

The trigeminal and facialis cranial nerve ganglia lie in a pocket formed within the lateral wall of the braincase. Presumably the outer wall of the pocket is formed by the processus ascendens palatoquadrati; the medial wall is endocranial. The pocket opens anteriorly into the endocranial cavity and nerve rami emerge from the pocket through three separate canals. An anterior canal (Fig. 32) carried the profundus V to its anterior opening into the jugular canal. A large laterally directed canal carried the r. maxillaris V and r. mandibularis V to an exit foramen in the temporal chamber. A third canal leads posteroventrally and seems to have carried the r. hyomandibularis VII. Immediately after the emergence of this canal from the trigeminofacialis chamber, a smaller canal divides off from the palatal region. This canal (Fig. 32) carried the r. palatinus VII. The canal for the r. hyomandibularis VII passes into the jugular canal. Apparently the nerve ramus ran across the canal and then passed ventrally into the tip of the spiracular cleft (Fig. 32). A second short canal (Fig. 32) carried the r. oticus VII which proximally must have run into the hyomandibular canal. There is no sign of a separate canal for the passage of the r. ophthalmicus superficialis VII; it seems most probable that this nerve emerged from the braincase through the maxillary-mandibular V foramen.

Occipital Region. Only one of the available specimens (F 10813A) shows any part of the occiput; in it only the anteroventral region and a small portion of the lateral wall are preserved (Figs. 75, 77; Figs. 78, 81; Figs. 82–84). A most interesting feature of the occiput is the presence, on each side of the specimen, of a sulcus passing behind the otic capsule through the anterior margin of the tenth cranial nerve foramen and ventrally behind the root of the otoquadrate bar to meet its fellow of the other side. It is tempting to regard this sulcus (Fig. 31, *sl;* Fig. 78) as representing the separation between the otic and occipital regions of the skull; for the purposes of description, this hypothesis will be followed here. The possible homology of this sulcus is considered further.

A second foramen for the tenth cranial nerve (possibly a superior lateralis ramus) is located midway up the lateral neurocranial wall, tucked under the posterior corner of the otic capsule. Just below this foramen is a vertical canal carrying the occipital artery into the endocranial cavity. Behind this point, the lateral braincase wall is extremely thin and delicate; only the ventral portion is more solid. On either side of the ventral occipital region, the wall of the neurocranium is continuous with that of the otic region and bears the posterior part of the groove marking the passage of lateral dorsal aorta. Ventrally, the lateral wall curves medially (Fig. 83) and then it passes dorsally again in the form of a delicate vertical lamina just lateral of the midline. The laminae from each side join in the midline, forming a narrow medial cleft in the ventral surface of the occiput (Fig. 84). In the midline itself there is a median vertical septum extending further dorsally from this point into the cavity for the notochord. The notochordal canal tapers sharply as it passes toward the otic region. Although it is imperfectly preserved in our material, there is an indication of an horizontal septum separating the canals for the notochord and brain-stem. It has not been possible to see if this horizontal septum meets the vertical septum that seems to divide the notochordal canal. The significance of the vertical septum and the medial cleft on the ventral surface of the occiput is not known. Presumably the paired structure forming the ventrolateral walls of the occiput and enclosing the median cleft between them is formed by the parachordals.

COMPARISON WITH OTHER PALEOZOIC DIPNOI

Dipnorhynchus lehmanni. We have studied the descriptions of *D. lehmanni* by Westoll (*in* Lehmann and Westoll, 1952) and Lehmann (1956) and the interpretations of these forms by Jarvik (1954). However, we are forced to conclude that many of the features identified in these accounts are so imperfectly defined on the specimen that their identity is uncertain at best. The following features may be compared with reasonable confidence. The anterior pterygoids ("vomers") are overlapped by the anterior portion of the palate; this is not seen in *Dipnorhynchus sussmilchi* but is seen in *Uranolophus* (below). The dental structure is different, with the presence of more definitely shaped subconical tubercles having the appearance of being arranged in three "radiating" rows. However, this pattern of lateral tubercles could presumably be derived by a relatively minor modification of the pattern in *D. sussmilchi*.

In the description of *D. lehmanni* the composition of the palate is far from clear. Westoll (*in* Lehmann and Westoll, 1952) has figured the palate with separate pterygoid and parasphenoid elements and also identified basipterygoid processes. He considers the structure clear enough to be "strong support" for the view that early Dipnoi had a kinetic skull with a divided endocranium as in Crossopterygii. Jarvik (1954) gives a sketch and photograph of a cast of the palate of *D. lehmanni*. He does not show any separation between parasphenoid and pterygoid nor does he identify the basipterygoid processes. We are inclined to accept this part of Jarvik's description and, since the skull of *D. lehmanni* is completely crushed, we consider it most probable that the ridges in the palate identified as the parasphenoid and basipterygoid processes are actually caused by the crushing of the palate into the endocranium. This does not mean that the parasphenoid is absent in *D. lehmanni*, but the available evidence seems to suggest that the palate in this form, as in other Dipnoi, is fused to the undersurface of the endocranium and shows no sign of kinetism. Jarvik (1954, figs. 36A, 37A) has also described in his casts of *D. lehmanni* a posterior projection from the palate, which he interprets as a posterior parasphenoid stalk comparable to that found in Middle Devonian and younger dipnoans. The accounts of Westoll and Lehmann give no sign of such a structure. It could equally well be an indication of the posterior part of the braincase (the ventral surface of which, as we have previously seen, is paired in *D. sussmilchi*). It is also not impossible that it is an artifact (see Lehmann *in* Lehmann and Westoll, 1952, for an account of difficulties encountered in preparing the material).

Until the details of the palate in *D. lehmanni* are more fully understood we continue to include it in the genus *Dipnorhynchus*, but with some reservations (see also discussion by Denison, 1968a).

Uranolophus. The otherwise rather well-preserved material of the oldest known dipnoan *Uranolophus wyomingensis*, as described by Denison (1968a, b), unfortunately does not reveal any details of the structure of the braincase except that both perichondral and endochondral ossifications were present. However, it is possible to make some useful comparative observations on the palate of *Uranolophus*.

The ventral aspect of the palate in the nasal region (Denison, 1968a, fig. 8) shows an arrangement of the nasal organ generally similar to that of *Dipnorhynchus*, or indeed most other fossil dipnoans. There is a prominent notch for the anterior naris: the posterior naris must have been located in the most posterior part of the capsule as Denison notes. It seems most probable that the solum nasi was present only in cartilage as in other forms. The median internasal septum is approximately as wide as in *Dipnorhynchus*, but no details of subdivision of the nasal chamber may be seen. The nasal capsule is relatively shorter than in *Dipnorhynchus*. The ventral bar of the postnasal wall is developed exactly as in *Dipnorhynchus*. In the palate there are separate vomers, pterygoids, and a median parasphenoid. The anterior pterygoids ("vomers") are more or less the same as in *Dipnorhynchus*, but there is no space between them and the pterygoids. Denison suggests that they were overlapped by the anterior margins of the pterygoids. As in *Dipnorhynchus* they partially underlie the nasal capsule. The parasphenoid is extremely broad in

Uranolophus and extends far forward between the pterygoids but has no posterior stem. In this last feature *Uranolophus* and *Dipnorhynchus* differ importantly from the later Dipnoi. There is no external hypophysial opening. The dermal bones of the palate in *Uranolophus* lack well-developed tooth plates, such as seen in later forms, but are covered with small denticles. Laterally a ridge on the side of the pterygoids forms the only modification of the essentially flat occlusal surface. This is also clearly a major point of difference from *Dipnorhynchus* and other known dipnoans.

As in *Dipnorhynchus*, the dorsal surface of the palate in *Uranolophus* is thickened to buttress the braincase underneath the postnasal wall and just in front of the optic nerve foramen. Also present in *Uranolophus,* but in no other known dipnoan except *Dipnorhynchus*, is the conical "lateral palatal process" which Denison (1968a) believed to be an additional point of support of the pterygoid but, as far as we can determine, does not attach to any other structure in either genus. The vascular and nervous system associated with the palate in *Uranolophus* cannot be fully identified, but the foramen for the arteria ophthalmica magna is seen in the floor of the orbital chamber, in the same position as in *Dipnorhynchus*. There is also an indication of the marked lateral groove passing around the margin of the anterior part of the palate under the postnasal wall, that is considered to have held a subnasal vein in *Dipnorhynchus* (see also *Ganorhynchus*, below). The overall similarity between *Dipnorhynchus* and *Uranolophus* with respect to the dorsal surface of the palate strongly suggests that the adductor muscle system and temporal chamber were essentially the same in the two genera.

Dipterus. Unfortunately, the amount of information that we have concerning the endocranium of the Middle Old Red Sandstone dipnoan *Dipterus* is very small in comparison with the extensive and finely detailed information that we have concerning the dermal bones of the skull roof. Woodward (1891), Goodrich (1909) Watson and Day (1916) Säve-Söderbergh (1952), Jarvik (1954, 1964), and Gross (1964) have provided partial information and restorations, but only White (1965) has been able to study material of the whole endocranium. White's specimen was incomplete in the nasal region, but we are able to describe here some details of the structure of this region from a study of a specimen from the Royal Scottish Museum (RSM 1859–33–612 *Dipterus valenciennesi*). From this new material and from Jarvik's study of the narial opening and upper lips, we are able to make a reasonably complete restoration of the anterior portion of the endocranium of this fish. Although Jarvik (1964) was able to describe the details of the narial openings in *Dipterus,* so far as we know, only one specimen exists that shows internal endocranial details in the rostral region. In this specimen the perichondral-bone lining of the dorsal surface of the nasal capsules has been eroded away, exposing the internal network of ramifying nerve and vascular canals (Fig. 30B, Fig. 68).

In most principal features the endocranium of *Dipterus* is similar to that of *Dipnorhynchus*. There are, however, significant differences between the two. The process behind the notch for the anterior naris (Fig. 30) is much smaller in *Dipterus*, and in other dipnoans (see p. 71) than in *Dipnorhynchus.* This is probably associated with the relatively larger extent of the nasal capsule in *Dipnorhynchus* than in later genera and may be connected with the development of a cartilaginous subnasal septum, extending medially between the two nares. The composition of the postnasal wall is shown best in White's account of *D. valenciennesi* (1965, figs. 43, 44). It is buttressed by a large process from the palate exactly as in *Dipnorhynchus* (although rather more strongly developed). It is not possible to distinguish an orbitonasal groove under the postnasal wall in *Dipterus*.

From White's description it is clear that in dorsal aspect the overall shape of the endocranium in *Dipterus* is generally similar to that of *Dipnorhynchus*. The dorsal margin of the lateral wing of the palatoquadrate is attached to the undersurface of the same dermal skull roof elements as in *Dipnorhynchus*. However, there may be differences in the otic and occipital regions. In White's specimen (P 17410) the simple medial dorsal septum that in *Dipnorhynchus* separates the chambers for the temporalis musculature of either side is not present. The skull of this specimen is relatively much lower and the temporalis chambers are separated by the neurocranium, which is applied directly to the undersurface of the skull roof itself. The neurocranium is wide in this region and contains a large cavity interpreted by White as containing a diverticulum of the endolymphatic duct. The chambers for the masseter and temporalis musculature are small in the otic region. Although the neurocranium is largely missing in the specimen of *Dipterus* mentioned previously in connection with the rostral anatomy, there is a definite indication on the underside of the dermal skull roof of both the dorsolateral cristae and a median crista. These are arranged as in *Dipnorhynchus* and are shown in Figure 68. The possibility therefore exists that in *Dipterus* there was a very low dorsomedian crista that has been crushed in specimen P 17410.

In lateral and ventral aspects, further important differences between *Dipterus* and *Dipnorhynchus* are seen. In *Dipnorhynchus* the quadrate articulation is located at the level of the center of the otic capsule and the posterior face of the temporalis chamber is essentially a vertical lamina. In *Dipterus* the posterior wall is inclined at an angle of approximately 45°, carrying the quadrate articulation forward to approximately the level of the profundus foramen. As a consequence, the cheek region is greatly reduced anteroposteriorly in *Dipterus*. The opercular chamber is modified accordingly, and we may note that the efferent pseudobranchial artery in *Dipterus* comes for part of its course to lie in a canal enclosed within the lateral palatoquadrate wing. There seems to be no lateral palatal process in *Dipterus*.

As far as may be discerned, the arrangement of the cranial nerve and vascular foramina in this orbitotemporal region of *Dipterus* is identical with that of *Dipnorhynchus* with only slight differences in position. On the posterior face of the palatoquadrate, however, there are important differences. The jugular vein passes backward through a jugular canal and then posteriorly in a groove on the lateral otic wall, but the hyomandibular nerve in *Dipterus* apparently left the endocranium through a foramen directly lateral to the posterior jugular foramen, and the orbital artery passed into the braincase at a point considerably ventral to these two foramina. No sign of a separate hyomandibular is present and one can only conclude that no hyomandibular structures have become incorporated into the braincase in any recognizable manner. If a hyomandibular had simply been fused into the posterior face of the palate, presumably the orbital artery would have continued to pass over it dorsally, as is the case in *Neoceratodus*. The only way in which one could satisfactorily accommodate the hyomandibular into the otic region would be if the canals for the orbital artery and hyomandibular nerve had been misinterpreted and were in fact reversed. However, their appearances in White's figures (1965, figs. 43, 46) belies this; furthermore, there is good corroborative evidence from the structure of another Devonian form, *Chirodipterus,* that White's identification of the hyomandibular nerve foramen is correct.

In ventral aspect also the endocranium of *Dipterus* differs in important features from that of *Dipnorhynchus*. The palatoquadrates and pterygoids in *Dipterus* are widely separated posteriorly from a point in front of the hypophysial opening. The latter is located far in advance of its position in *Dipnorhynchus* and lies in the anterior part of a large rhombic parasphenoid that extends posteriorly under the otic region. This is also a product of the proportional changes by which the quadrate articulation is brought forward, leaving a considerable ventral surface behind the palate.

Ganorhynchus. In 1965, Gross described certain features of the anatomy of the rostral region in the upper Middle Devonian dipnoan *Ganorhynchus splendens* Gross. In many ways there is considerable resemblance between the structures seen in the nasal region of this form and that of *Dipnorhynchus sussmilchi*. The nasal cavity in *Ganorhynchus* is partially subdivided into three portions that correspond exactly to the anteromedial, anterolateral and posterior recesses of *Dipnorhynchus*. The arrangement of the small canals piercing the tectum nasi in *G. splendens* is rather different from that of *D. sussmilchi*.

The postnasal wall in *G. splendens* is pierced by two important canals. The first is easily homologized with the profundus canal of *D. sussmilchi*. The second is a canal of varying manifestation termed the orbitonasal canal by Gross and homologized with the similarly named canal in *Chirodipterus* (see below). On the left side of Gross' specimen this canal passes ventrally and medially of the profundus canal to emerge into the ventromedial corner of the nasal cavity and passes along the lateral side of the palate in a elongate groove. On the right side of Gross' specimen (wrongly labelled in his figure 1, 1965; personal communication) the relative positions of the profundus and orbitonasal canals are different. The profundus is situated slightly medially of the orbitonasal canal, but the latter nonetheless leads anteriorly into a groove along the side of the tip of the palate. In *Ganorhynchus*, exactly as in *D. sussmilchi*, two canals on each side lead directly forward from the anteromedial recess into the region which in *Dipnorhynchus* is occupied by the rostral tubuli. Also, as in *Dipnorhynchus*, the internal septum is more complete posteriorly, and anteriorly it is present only as a dorsal band. In *Ganorhynchus* the canals for the olfactory tracts merge together at the level of the postnasal walls, while in *D. sussmilchi* they fuse somewhat further posteriorly. In *Ganorhynchus* the palatal dentition extends anteriorly underneath the septum nasi, considerably further than in *Chirodipterus* and approximately to the same extent as in *Dipnorhynchus*. It seems possible, therefore, that the sharply pointed tip of the palatal dental battery includes a pair of "anterior pterygoid" elements similar to those of *Dipnorhynchus*.

Chirodipterus wildungensis. The first full description of the endocranial anatomy of a fossil lungfish was given by Säve-Söderbergh (1952) in a beautifully detailed account of the lower Upper Devonian genus *Chirodipterus* from Wildungen in Germany.

In many features the anatomy of *Dipnorhynchus* is remarkably similar to that of *Chirodipterus*. Several of the features in which the two differ demonstrate clearly the more primitive nature of *Dipnorhynchus* and aid our interpretations of the later forms.

Whereas the ethmoidal region in *Dipnorhynchus* is somewhat flattened in transverse section, that of *Chirodipterus* is strongly rounded. The arrangement of the "lips" around the dorsolateral surface of the endocranium is remarkably similar in the two genera. From the new information that is available concerning the position of the narial openings in *Dipnorhynchus* and *Dipterus* we may see that the posterior naris in *Chirodipterus* must have had a similar position. The notch in the lateral margin of the snout that lies immediately behind the notch from the anterior naris did not house the posterior naris, as previously suggested (Thomson, 1965), but rather the small element supporting the upper lip (see especially Jarvik, 1964). As in other known forms, there is no sign of a ventral wall to the nasal capsule in *Chirodipterus*. The internasal septum is similar to that of *Dipnorhynchus* being complete dorsoventrally only in the posterior portion of the nasal region. The deep recess from the posterior corner of the nasal cavity into which the olfactory tract opens in *Dipnorhynchus* is not developed in *Chirodipterus* (see Säve-Söderbergh, 1952, fig. 3); there seems no indication of any subdivision of the nasal cavity into the three recesses seen in *Dipnorhynchus*. Few canals or foramina in the dorsal nasal roof are illustrated by Säve-Söderbergh, but an interesting feature is the presence of two major canals in the postnasal wall. The first of these is readily identified as the profundus canal, which seems to divide within the postnasal wall and emerge into the cavity by three separate foramina. The second canal is an enigmatic structure that Säve-Söderbergh termed the orbitonasal canal. It apparently connects three separate foramina in the posterior face of the postnasal wall to a single internal foramen in the medial corner of the nasal cavity where it leads into a groove passing around the medial surface onto the side of the septum nasi. The significance of this structure (which is also seen in *Ganorhynchus,* see p. 83) is difficult to determine. However, it seems unlikely that it contained any nerve. The groove on the posterior medial corner of the nasal cavity into which the orbitonasal canal passes, however, is remarkably similar to the lateral subnasal groove on the side of the palate in *Dipnorhynchus*. This resemblance is even more marked in the specimen of *Ganorhynchus* described by Gross (1965). In *Dipnorhynchus* this groove seems clearly to have carried elements of the venous system backward from the nasal region to the suborbital sinus. Under the postnasal wall it receives several small veins from the palate and also (Fig. 29) from the postnasal wall itself. It seems possible that the orbitonasal canal of *Chirodipterus* and *Ganorhynchus* also carried veins backward from the nasal region. In this case it would be necessary to explain why the canal turns to enter the postnasal wall instead of continuing beneath it as in *Dipnorhynchus*. This may be partly explained by an increased development of the palatal buttress under the postnasal wall in the younger forms so that there is less space beneath it. It may also be significant that the canal for the ramus maxillaris V in *Dipnorhynchus* is widely separated from the vascular groove discussed above, while in *Chirodipterus* it is associated extremely closely with the orbitonasal canal and in *Ganorhynchus* the orbitonasal canal is undivided and the canal for the r. maxillaris V does not seem to be present. Possibly the orbitonasal canal of *Chirodipterus* and *Ganorhynchus* represents a passageway for veins leading from the nasal region to the suborbital sinus, perhaps running in conjunction or close association with the maxillaris V nerve.

In the general composition of the orbitotemporal region there is remarkable agreement between the structure of *Dipnorhynchus* and *Chirodipterus,* with an identical arrangement of the optic, third and fourth nerves, the canal and foramen for the ophthalmica magna artery, the pituitary vein, profundus-jugular canal foramen, trigeminal nerve foramen and orbital artery. Internally the composition of the trigeminofacialis ganglion recess is different, in that the vena cerebralis medialis is closely associated with the seventh cranial nerve (r. hyomandibularis), while in *Dipnorhynchus* this vein seems to enter the jugular canal separately and somewhat posteriorly. The jugular canal has the same relationship to the trigeminofacialis ganglia and nerves. The canal for the ramus palatinus VII in *Chirodipterus* apparently also enters the jugular canal for a short distance. The anterior face of the lateral wing of the braincase stands at an angle of about 75°, compared with 90° in *Dipnorhynchus* and 45° in *Dipterus.*

The arrangement of the dorsomedian and dorsolateral cristae is the same in the two genera, as is the general structure of the inner ear.

An important difference between *Dipnorhynchus* and *Chirodipterus* is to be found in the structure of the posterior face of the palatoquadrate. In *Chirodipterus* the massive otoquadrate structure seen in the former genus is absent. However, it is interesting that in this form the posterior openings of the canals for the jugular vein and the orbital artery are separate, while they are connected briefly internally where the hyomandibular nerve apparently transfers its course from one canal to the other. This is what one would expect to be the situation if the hyomandibular had been lost from the endocranium. If the hyomandibular were simply incorporated into the endocranium one might expect to see a common external posterior foramen for the jugular vein and orbital artery. Furthermore, there seems to be no sign in *Chirodipterus* of a spiracular cleft.

The internal carotid artery in *Chirodipterus* passes forward externally to the braincase, only entering it just behind the hypophysial foramen, the latter being relatively anterior in position. This is in accordance with the relatively weaker development of the palatoquadrate (basal processes) and the presence of a median posterior parasphenoid, over the exposed ventral neurocranium.

In *Chirodipterus* there is a well-marked canal and groove system for the passage of the first efferent arterial arch, cutting through the posterior portion of the palatoquadrate. This vessel is more free in *Dipnorhynchus.* In the palate of *Chirodipterus* the entopterygoids reach backward as far as the glenoid articulation. In *Dipnorhynchus,* as previously noted, there is an area of exposed quadrate opposite a small shelf on the hind margin of the lower jaw forming the attachment for a palatomandibular ligament.

General Comparison. Two points of general interest with respect to the comparison of fossil dipnoan skulls may be made here. The first is that in all known forms the position of the narial apertures and the arrangement of the nasal apparatus are similar. Particularly, the nares are always on the underside of the snout and

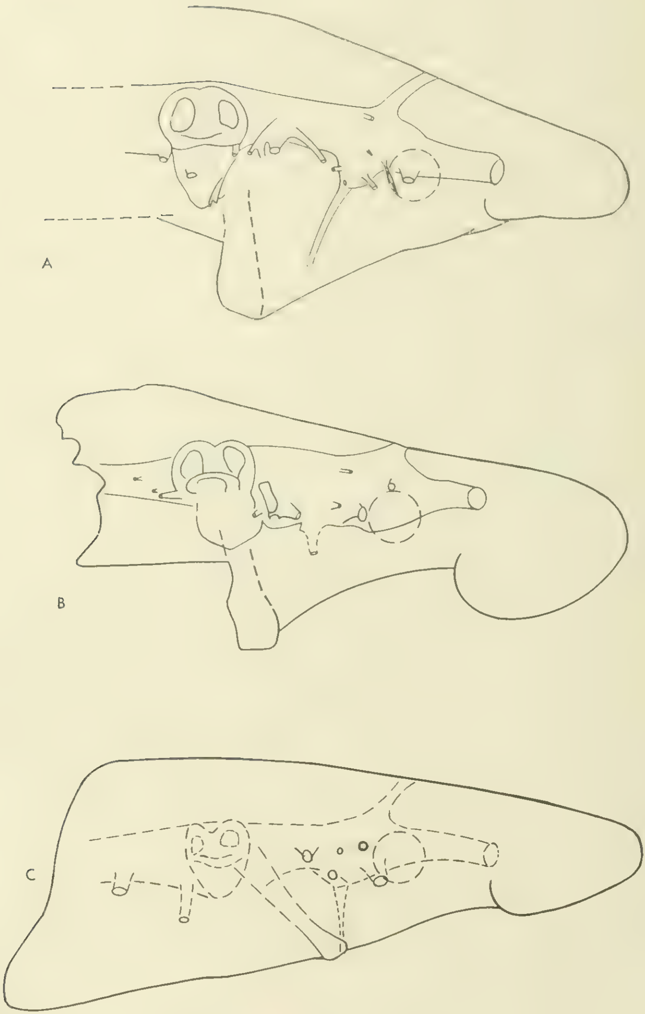


FIG. 33. Comparison of the proportions of the braincase in three Devonian Dipnoi: A) ***Dipnorhynchus sussmilchi;*** B) ***Chirodipterus wildungensis*** (after Säve-Söderbergh, 1952); C) ***Dipterus valenciennesi*** (reconstruction after data in White, 1965).

the snout always overhangs the oral opening. It has been suggested previously (Thomson, 1965; Panchen, 1967) that the ventral orientation of the nares in Dipnoi is a primitive feature. The present evidence offers some slight additional support for this view. There is no evidence in the newly available materials of primitive Dipnoi that the nares have migrated from a more "normal" osteichthyan position on the lateral surface of the head (cf. Jarvik, 1942; Lehmann and Westoll, 1952). Obviously this arrangement of the nasal apparatus must be connected with the lack of a marginal dentition in the Dipnoi.

The second point of general comparison involves the relative proportions of the skull in early Dipnoi. This has been a problematic subject, with several authors offering opposing views of both the evidence and its interpretation (Westoll, 1949; Denison, 1968a; Jarvik, 1968). The principal questions have concerned the relative proportions of the otic region of the skull and of the cheek. However, it is necessary here to draw attention to the relative proportions of the entire braincase in the available early Dipnoi. In Figure 33 the principal features of the braincase (nasal capsule, cranial nerve foramina, otic capsule, together with the position of the fused posterior wall of the palatoquadrate) are compared in *Dipnorhynchus, Chirodipterus,* and *Dipterus*, with details of the endocranial cavity included for the first two genera. It will be seen from Figure 33 that—despite Westoll's interpretation (1949) that the otic region becomes shorter in the early history of the Dipnoi and Jarvik's opinion (1968) that it becomes longer—the new evidence shows that the proportions of the braincase in these forms are essentially constant. There are, indeed, small differences in the position of the optic nerve foramen and the angle of the posterior wall of the palatoquadrate. The latter is obviously responsible for the changes in the proportions of the dermal cheek series. There are also differences in the relative size of the nasal capsule. However, this series of three genera, in which there is a considerable change in the pattern of the dermal skull bones, gives no evidence here of any incipient phyletic trends in braincase proportions.

Since these are the only fossil Dipnoi in which the details of the braincase and cranial nerve foramina are known, it is methodologically invalid to attempt to draw any phyletic inferences from comparison of these forms and the living genera. It may well be true (Säve-Söderbergh, 1952; cf. Jarvik, 1968) that the labyrinth cavity in *Neoceratodus* is slightly bigger than in *Chirodipterus,* but this is obviously not *by itself* evidence of a general trend toward increase in the relative size of the otic region during the period between Devonian and Holocene.

EMBRYOLOGICAL ANALYSIS OF BRAINCASE

In view of the considerable morphological significance of the structure of the skull of *Dipnorhynchus* and of primitive osteichthyans in general (see, for example, Schaeffer, 1968), it seems worthwhile to attempt to analyze the complicated holostylic skull of *Dipnorhynchus* in terms of the probable embryonic components.

In the nasal region, identification of the principal embryological components that have entered into the formation of the adult structure is relatively simple. The trabeculae of the anterior neurocranium pass forward probably fused as trabecular horns into the nasal region. The internasal trabecular extension curves forward dorsally between the nasal organs forming the dorsal portion of the internasal septum preserved as bone in the fossil. From this ethomoidal plate a cartilaginous septum possibly extended ventrally to complete the internasal septum between the anteromedial portions of the nasal organs. Anteriorly, the trabecular region curves ventrally and then the lateral horns curve laterally to form the anterolateral corner of the roof of the nasal cavity anterior to the anterior naris.

It has been noted in a previous study (Thomson, 1965) that the contribution of the trabeculae to the internasal septum differs in the living Dipnoi. In *Protopterus* and *Lepidosiren* the anterior portions of the trabeculae fuse to form a median structure which curves dorsally over the internasal region. A secondary septum then reaches down ventrally between the nasal sacs to form the internasal septum. Anteriorly the trabecular portion curves ventrally again and gives off the trabecular horns. In *Neoceratodus* the trabeculae reach directly forward in the floor of the nasal region and the internasal septum is developed as a dorsal extension from them. The preserved portion of the incomplete internasal septum of all known fossil Dipnoi (*Dipnorhynchus*, *Uranolophus*, *Ganorhynchus*, and *Chirodipterus*) is arranged in the same way as in Lepidosirenidae, with a dorsal band of tissue curving over the nasal region. It seems a reasonable conclusion that the preserved portion of the internasal septum in these fossil forms actually represents material of trabecular origin. In this case, the arrangement of the trabeculae in the internasal region of *Neoceratodus* must be considered as secondary.

The prominent ventral bar of the postnasal wall is formed by the processus antorbitalis from which a dorsal lamina extends to form the postnasal wall around the profundus canal. The lateral wall of the capsule is formed by the fusion of the processus antorbitalis with the recurved trabecular horn. They fuse dorsal to the narial apertures and there is accordingly no continuation of this lateral wall ventral to this level. The processus antorbitalis also has a posterior distal fork that forms the buttresses against the undersurface of the skull roof. It would perhaps be an optimistic anatomist who would find homology between the forked end of the processus antorbitalis in *Dipnorhynchus* and that in *Lepidosiren* (as described by Agar, 1906a).

The strong direct connection between the undersurface of the postnasal wall (lamina orbitonasalis) and the visceral palate might perhaps be construed as evidence for the suggestion by Jarvik (1954; cf. Bertmar, 1963) that the lamina orbitonasalis in fishes is of visceral origin.

In the orbital region the separation between palatoquadrate and neurocranial components probably ran on a horizontal level ventral to the optic foramen. In the temporal and otic regions the separation is more difficult to determine. The jugular canal seems to be formed by the apposition of a processus ascendens palatoquadrati laterally with the neurocranial wall medially. The maxillary-mandibular fifth nerve foramen marks the separation between the processus ascendens and processus oticus palatoquadrati. The latter is fused to the anterolateral wall of the otic capsule and forms the lateral wall of the posterior section of the jugular canal. The dorsal extent of the processus oticus cannot be determined, but presumably the dorsolateral crista of the endocranium is a neurocranial structure. As we have seen, the trigeminofacialis ganglion complex lies dorsal to the jugular canal, but it must be considered to be enclosed laterally by both the processus ascendens and processus of the palatoquadrate, with the maxillary-mandibular foramen between them. The question of whether there is a lateral commissure or a cavum epiptericum is formed between the palatoquadrate and neurocranium is one that cannot be answered until the homology of the "otoquadrate bar" has been decided.

Ventrally, the palatoquadrates are extremely thick underneath the otic region and are greatly expanded both toward the midline where they fuse beneath the neurocranium (enclosing the internal carotid arteries) and posteriorly where they are seen to spread backward underneath the otic region. The expanded medial parts of the palatoquadrates correspond to the basal palatal processes and their extreme enlargement essentially obliterates the basal plate of the trabecular neurocranium. It will be noted, from the posterior position of the hypophyseal recess and canal and the position of the tip of the notochord, that the trabecular portion of the neurocranium extends far posteriorly, to approximately the level of the center of the inner ear cavity. Underneath the occipital region the paired ventral structures presumably represent the main parts of the parachordals on either side of the notochord.

The trigeminal and facialis nerve ganglia are enclosed in a portion of the braincase wall, the outer part of which is probably palatal in origin. The jugular canal also is enclosed laterally by the palate. However, a point of difference from other fishes is that none of the fifth nerve rami pass directly into the jugular canal, the course of which lies morphologically ventral to the level of the ganglion complex. The profundus nerve only enters the jugular canal at the anterior jugular foramen. The ramus hyomandibularis VII passes posteriorly into the jugular canal. Both nerves seem to pass for a distance within the substance of the braincase wall dorsally and slightly medially of the jugular canal. The possibility exists that this portion of the braincase wall, immediately ventral to the trigeminofacialis ganglion pocket, is formed embryonically of two parts, medial neurocranial and lateral palatal structures—between which the previously mentioned nerves pass.

BRANCHIAL SKELETON OF *DIPNORHYNCHUS SUSSMILCHI*

In the material that we have prepared there is a single element that we have tentatively identified as a portion of the hypobranchial skeleton. This small element is illustrated in Figure 34 (reconstruction) and in Figure 90a, b, c. Although incomplete, the specimen represents a portion of a bilaterally symmetrical element that we assume to have been a basibranchial located in the ventral midline. It consists of a central disc, dorsally concave, to which a series of rod-shaped elements (the tips of the hypobranchial elements) were attached. One such element is preserved in natural association on the right-hand side. A facet showing the position of attachment of a symmetrical left element is clearly shown. In addition, on the ventral face of the disc there is a median facet that formed the site of attachment of a more ventral element (presumably a urohyal) pointing directly backward in the midline. The base of the preserved portion of the right hypobranchial shows a further site of attachment, presumably for the next most anterior arch. Anteriorly, the disc-shaped base is incomplete; we imagine that it was attached to a more anterior basibranchial. In our interpretation, the preserved element supported the urohyal and branchial arches IV and V. The anterior basibranchial supported the remaining elements.

The branchial skeleton of other Palaeozoic dipnoans is, unfortunately, unknown.

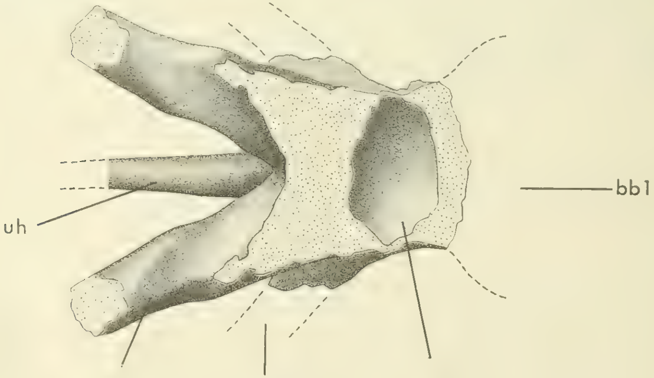


FIG. 34. *Dipnorhynchus sussmilchi.* Reconstruction of portion of the hypobranchial apparatus, based on specimen P 13837, National Museum, Melbourne.

SQUAMATION OF *DIPNORHYNCHUS SUSSMILCHI*

Two different types of scales of *Dipnorhynchus sussmilchi* are available for study. Several rhombic flank scales were discovered in association with the lower jaw from Buchan (P 13837), a single incomplete flank scale was embedded in the matrix on specimen F 10813 [this was interpreted by Hills (1933) as forming part of the denticulation of the palate], and an isolated median dorsal ridge scale was collected as Taemas (1970D) by Dr. J. A. Warren. The scale structure is illustrated in Figures 86 to 89.

The flank scales show a remarkable structure, for dipnoans, in that they articulate one with another by means of the "peg-and-socket" arrangement that was long ago considered diagnostic of the "ganoid" fishes (see "Discussion"). The dorsal margin of each scale is produced into a short roughly triangular "peg" which fitted into a simliarly shaped depression in the ventral part of the undersurface of the scale in the next row. The depression or "socket" is actually formed on a broad dorsoventrally directed thickened band on the internal face of the scale. The "peg" is the dorsal projection of the thickened band beyond the margin of the scale surface. The surface of this median thickened band of tissue is marked by a series of parallel ridges (Fig. 86b).

The external face of the scale is formed in two discrete areas. The anterior portion of the scale—the narrow area that was overlapped by the scale in front—is covered with closely spaced, flattened dentine tubercles. This tuberculated area extends dorsally in a narrow band just at the base of the "peg" process. The exposed portion of the external face of the scale is cosmine covered, and "Westoll-lines" may be observed. In certain cases, abrasion of the surface of the scale has removed part of the cosmine surface, and the denticulated dentine layer beneath is revealed (Fig. 89a). The histological nature of these features is described below.

The rhomboid shape of the scale and the "peg-and-socket" type of articulation has been described in the Middle Devonian osteolepid rhipidistians *Gyroptychius* and *Osteolepis (*Jarvik, 1948). It has also very recently been described in the primitive lungfish *Uranolophus* (Denison, 1968a, b). Like *Uranolophus, Dipnorhynchus* lacks the groove separating the cosmine-covered and denticulated areas on the outer face of the scale which is seen in the above-named rhipidistians. But whereas the ridge on the inner surface of the scale is "weak or absent in *Uranolophus*" (Denison, 1968a), it is as well developed in *Dipnorhynchus* as in Rhipidistia. The overall similarity in general structure of the scales of these forms is most striking as is the difference between this type of scale and that seen in the later Dipnoi.

NOTES ON BONE HISTOLOGY OF *DIPNORHYNCHUS SUSSMILCHI*

We have already noted that cross sections through the massive palate of *Dipnorhynchus sussmilchi* show that it is composed primarily of a thick layer of spongy endochondral bone on the ventral surface of which is a layer of dentine. There was possibly an external enameloid or durodentine layer, but the preservation makes the identification uncertain. The dorsal surface of the palate was formed by a thin perichondral bone layer.

We have made thin sections of a portion of the surangular bone of specimen P 13837 from Buchan. The basal layer of the dermal bone is made up of lamellar bone showing cross striations; next there is a fairly thick layer of spongy bone; and on top of this lay dentine and cosmine layers. On the dentary, the tip of the snout, and most of the surface of the prearticular there was an enamel surface.

The composition of the scales is generally similar to that of the dermal bones. There is a very thick lamellated, cross-striated basal layer separated by a thin spongy bone layer from the more external dentine. The dentine seems to be orthodentine. The surface of the shiny exposed portion of the scales is formed of cosmine. The tubercles on the overlapped portion of the external surface are formed of dentine only. Under the smooth cosmine layer, several generations of overgrown denticles may be seen. The "Westoll-lines" may also be detected in thin sections.

These notes are unfortunately brief owing to the less than perfect state of preservation of microscopic detail in the material. In every feature that has been examined, however, the histology shows a remarkable resemblance to that seen in *Uranolophus* and described by Denison (1968a). As far as we can tell, Denison's observations on structure and growth in *Uranolophus* must apply equally to *Dipnorhynchus*. The occurrence of an enamel layer on the snout, dentary, palate, and prearticulars seems to be a common phenomenon in Devonian Dipnoi.

NOTES ON SOFT ANATOMY OF *DIPNORHYNCHUS SUSSMILCHI*

Reconstructions of the soft anatomy of a fossil organism are, of course, highly tenuous and usually suffer from the fact that they are based on extensive extrapolations from conditions in living forms. However, it is important that attempts at reconstruction be made and accordingly we present the following notes on selected aspects of the soft anatomy of *Dipnorhynchus.*

NASAL ORGAN. As already described, the nasal organ lies in a nasal chamber that is partially subdivided into three main portions–a principal posterior chamber and smaller anteromedial and anterolateral chambers. These chambers must reflect a similar subdivision of the nasal organ itself. The anterolateral chamber is directed anteriorly towards the notch in the margin of the snout that must have (partially) enclosed the anterior naris. The position of the posterior naris is not indicated by such a notch, and we may be certain that the posterior naris must have been situated in the ventral part of the principal posterior portion of the nasal organ. An important feature to notice is that both the narial openings are completely ventrally directed and the position of the nares is identical with that in other Dipnoi. It is difficult to assign a particular functional significance to each of the three subdivisions of the nasal organ. The anterior recess seems to be principally the anterior portion of the original "nasal groove." The position of the posterior naris given in the restorations (Fig. 27) places the posterior end of the nasal groove at the junction between the end of the anterolateral portion of the nasal organ and the posterior portion. The latter is clearly the main sensory region of the nasal organ and possibly contained a rosette of olfactory surfaces. The olfactory tract enters the principal posterior section directly; the fact that the canal for the tract is subdivided by a thin vertical septum probably indicates that the dendritic branching of the olfactory tract over the whole of this sensory region occurs in the rearmost part of the nasal cavity. Although it would be tempting to try to identify a structure corresponding to Jacobson's organ in *Dipnorhynchus,* there is no justification for this. In fact, the existence of such an organ in living Dipnoi, or indeed any fish, is to be doubted (see Rudebeck, 1944; Thomson, 1965).

ACOUSTICOLATERALIS SYSTEM. The general structure of the inner ear and the cranial lateral line system of *Dipnorhynchus* have already been described previously. However, two aspects of the acousticolateralis system require further treatment.

SPIRACULAR SENSE ORGAN. In the preceding description of the otic region of the skull, we have identified a spiracular recess that we believe contained a spiracular sense organ leading from the spiracular cleft, the cavity of which was continuous with that of the pharynx. This identification is based upon the following pieces of evidence.

1) Its overall position is between the hyoid arch (behind) and the palatoquadrate (in front).

2) The hyomandibular ramus of the seventh nerve passes into the cleft.

3) Apart from the connection via the seventh nerve canal, there is no connection between the blind cleft and the neurocranial cavity, nor does it connect with the orbitotemporal cavity. Thus it cannot be the passage for any blood vessel.

4) A small ramus oticus VII passes into the posterior part of the spiracular cleft.

5) The internal faces of the cleft are extremely smooth, as if some soft structure were contained therein.

6) A spiracular sense organ has been identified in *Protopterus* and *Lepidosiren* (Agar, 1906b). A blind spiracular cleft has been described in embryos of *Neoceratodus* (see Fox, 1965). Although such an organ is not found in any other fossil dipnoan it is not an uncommon feature in other primitive fishes (Crossopterygii, *Amia, Lepisosteus,* etc.).

ROSTRAL TUBULI. As previously mentioned, at the tip of the snout and of the mandibular symphysis there are large external pores opening into a series of ramifying tubules which do not form part of the lateral-line system. These tubuli are formed of a perichondral bone sheath; they extend internally to open into the nasal cavity and Meckelian vacuity respectively, where they appear to receive a vascular supply and innervation from the fifth and or seventh nerves or both. The tubules are arranged very differently from the canals and pits that held neuromasts of the lateral seismosensory system. The rostral tubuli clearly housed a sensory system, but one may only guess at its specific function. Possibly it was in some way similar to that of the organs of Lorenzini.

DISCUSSION—EVOLUTION OF THE DIPNOI

Dipnorhynchus AND THE PHYLETIC POSITION OF THE DIPNOI. The question of the phylogenetic position of the Dipnoi has long been debated both with respect to their relationship to fishes in general and to the Amphibia in particular. It is now generally agreed that there was no direct relationship between Dipnoi and Amphibia (however, see Fox, 1965, for recent arguments in favor of such a link). But even after it had been found that the rhipidistian crossopterygian fishes provided a closer link to the earliest tetrapods than the Dipnoi, the problem of evaluating evidence for a possible dipnoan-crossopterygian relationship remained. Some workers, for example Goodrich (1909) and Woodward (1891), have classified the Dipnoi near the Arthrodira. Others, (particularly Westoll, 1949) have defended the concept of a natural assemblage containing the Dipnoi and Crossopterygii, and Romer (1955) coined the term "Sarcopterygii" for this group. Romer's view has prevailed with the majority of workers, but more recently Jarvik (e.g., 1964) has revived the possibility of a closer link of the Dipnoi to "elasmobranchiomorphs." White (1965, 1966) concurred with Jarvik, stressing particularly the distinctness of the dermal skull roof pattern and dentition. Bertmar (1968) argued that the closest relationship was between Dipnoi and Actinopterygii. Even more recently, Denison (1968a, b) and Schultze (1970) have brought forth new evidence that supports the sarcopterygian concept. The structure of *Dipnorhynchus sussmilchi* also provides strong evidence for a direct dipnoan-crossopterygian relationship (see also Thomson, 1969).

In comparison with other fishes, one fact is clear from the outset—that *Dipnorhynchus* is typically dipnoan. It has a primitive but nonetheless characteristically dipnoan skull roof and an apparently very primitive dipnoan dentition. However, it must be noted at the same time that in certain features *Dipnorhynchus* shows a structure that is not found in other dipnoans, but that is more typically found in the Crossopterygii. From these features we conclude that *Dipnorhynchus* is extremely primitive and shows evidence of a close phylogenetic relationship to the Crossopterygii or, more realistically, to the immediate ancestors of that group. We may now consider these in detail and try to assess their significance.

SCALES. The new descriptions of *Dipnorhynchus* and also *Uranolophus* (Denison, 1968a, b) have provided further new evidence of dipnoan-crossopterygian similarity. The microscopic structure of the scales, revealing traces of several generations of overgrown dentine tubercles, is remarkably similar to that described for the early rhipidistian *Porolepis* (Gross, 1956). The major structural features, particularly the "Westoll-lines" that show the manner of growth of the cosmine layer, and the peg-and-socket articulations between scales is the same as those seen in such Middle Devonian osteolepid rhipidistians as *Gyroptychius* [see also discussion by Denison (1968a, b)].

CHEEK. Whereas the cheek in all previously known Dipnoi is relatively short, *Dipnorhynchus* has a longer cheek, more readily comparable with that of other fishes such as the Crossopterygii. An important feature of the cheek is the presence of a short "preopercular" lateral-line canal in addition to the infraorbital canal.

LOWER JAW. The structure of the lower jaw in most dipnoans shows almost no resemblance to the lower jaw of other osteichthyan fishes, both with respect to the general arrangement of the dermal bones and the unique dental plates. The arrangement of the dermal bones of the jaw in *Dipnorhynchus* (and possibly *Uranolophus*), as we have seen, is more primitive than that of other dipnoans, but a scheme of evolution may be drawn up linking the structure of *Dipnorhynchus* and later forms in a common pattern (Fig. 24). Most importantly, it is also possible to see in the structure of *Dipnorhynchus* clear links with the arrangement in Crossopterygii. In Fig. 24 we compare the external dermal bones of the lower jaws of *Dipnorhynchus* and the rhipidistian crossopterygian *Holoptychius*. It is most remarkable how similar the two forms are, the only major divergence being in the relative development of the dentary, which in *Holoptychius* extends along almost the entire dorsal margin of the jaw and is readily correlated with the presence of a marginal dentition in Crossopterygii. A most striking point of similarity is the fact that the surangular in *Holoptychius* (though by no means in all crossopterygians) bears a short anterodorsal branch of the lateral line that is possibly homologous with the oral lateral line that in *Dipnorhynchus* is carried on the large surangular all the way to the anterior union with the mandibular lateral line. Although they had probably evolved separately from a common ancestor, one might easily suppose that the elongate *Holoptychius*-type of jaw evolved from the *Dipnorhynchus*-type by reduction of the surangular, enlargement of the dentary, and reduction of the symphysis. Although it is rather too early to decide which pattern is the more primitive, the presence of a full oral and a mandibular lateral line in the dipnoans raises the interesting possibility that this is the more primitive condition. Further it is possible that the dentary was originally a small anterior element, which only assumed its modern aspect as the principal tooth-bearing element of the lower jaw in the Osteichthyes as a specialization. A further point of resemblance between *Dipnorhynchus* and other Osteichthyes with respect to the lower jaw is the presence of a full Meckelian fossa (reduced in later Dipnoi).

In summary, despite the obvious differences in the dentition itself, the overall structure of the lower jaw of *Dipnorhynchus* is such as to form a common pattern with the Crossopterygii, while at the same time there are extremely clear relationships to the other Dipnoi.

These are all new evidences of similarity pointing to a direct and close relationship between Dipnoi and Crossopterygii. To these must be added Denison's (1968a, b) evidence from the structure of the postcranial skeleton of *Uranolophus* and Schultze's arguments (1970) concerning vertebral structure. When all this is added to the familiar lines of argument involving the presence of lungs, the development of the heart and brain, etc. cited by earlier authors, there is formed a substantial body of evidence suggesting (but, of course, still by no means proving) that the Sarcopterygii is a natural assemblage of closely related fishes, distinctly separated from other groups.

In order for this assessment of dipnoan-crossopterygian relationships to have authority it is necessary to provide, in addition, a satisfactory explanation of the major differences between the two groups—the differences that have led previous workers to separate them. The principal differences between the Dipnoi and Crossopterygii concern the skull (particularly the skull roof) and the dentition (see White, 1966). The characteristic nature of the skull of Dipnoi is obviously related to the phenomenon of holostyly. To understand the phylogenetic significance of these characteristics we must make some observations of the probable history of the skull in the ancestral predipnoan lineage.

Regardless of the interpretation of the "hyomandibula" in *Dipnorhynchus,* in our opinion, it seems most likely that in the immediate ancestors of this genus some mobility of the cheek upon the skull was possible (see Thomson, 1969), requiring the arrangement of an hyomandibula in a normal hyostylic or amphistylic suspension. The possible retention of a large distinct hyomandibular in the nonkinetic skull of *Dipnorhynchus* might be explained by its position, which indicates that it has taken on the function of bracing the posterior surface of the massive lateral wing of the braincase. If this is true, then it must follow that originally the palates were not completely fused. In any case, the separate parasphenoid, as developed in *Uranolophus* and possibly in *Dipnorhynchus lehmanni,* must be a primitive character that has become lost in *Dipnorhynchus sussmilchi.* However, there is no evidence to suggest that a posterior stem of the parasphenoid was present in a common ancestor. Had it been present, it surely would have been retained even in *Dipnorhynchus,* and certainly in *Uranolophus.* We may be reasonably certain that there was no posterior dermal covering in the roof of the gullet except for a pair of loose plates and the dermal elements (if any) directly associated with the branchial arches. Thus, the posterior process of the parasphenoid seen in Middle Devonian and younger dipnoans is a secondary feature. In this respect, the evolution of the dipnoan parasphenoid accords very well with Jarvik's scheme of the evolution of the parasphenoid in the Osteichthyes (1954).

The question of whether the skull in the earliest Dipnoi included an intracranial joint [such as was hinted at for *Dipnorhynchus lehmanni* by Westoll (in Lehmann and Westoll, 1952)] is impossible to decide. On the whole it seems likely that the jointed condition is a specialization of the Crossopterygii, as the holostylic condition is a specialization of the Dipnoi. However, even if an earlier dipnoan than *Dipnorhynchus* or *Uranolophus* had possessed an intracranial joint, no indication of it would be expected to be retained in these heavily holostylic forms. In the absence of more primitive dipnoans, this question must be left unresolved.

Apart from the "normal" movements between cheek, palate, and braincase that are seen in many fishes, the possibility also exists that in an early form the otic-occipital connection (represented by a sulcus in *D. sussmilchi*) also allowed some degree of intracranial flexure. In this case, the absence of a posterior parasphenoid stalk, which braces the ventral surface of this region in later Dipnoi, would further be explained. The fact that a somewhat similar otic-occipital sulcus is found in paleoniscid actinopterygians may suggest that such structures were a primitive feature of all Osteichthyes. If this were the case, then probably the crossopterygian kinesis at the trabecular-parachordal separation represents a lateral innovation.

If there were some kind of intracranial movement in ancestral dipnoans, then the very rapid evolution of the characteristic holostylic dental battery, which is evident from the stages reached by *Uranolophus* and *Dipnorhynchus*, must have taken place *after* the Dipnoi differentiated from the ancestral stock. Probably any marginal dentition was lost at a stage when it was only feebly developed—as indicated by the short dentary in *Dipnorhynchus* and the primitive ventral position of the nares in Dipnoi (see also Thomson, 1965).

If the preceding assessments are correct, then we may make two observations concerning the phylogenetic significance of the specialized dental apparatus of Dipnoi. 1) Since the dipnoan dental pattern is a specialization that probably developed *within* the Dipnoi, rather than was present in an antecedent stock, it would be wrong to argue that this characteristic provides evidence that the Dipnoi and Crossopterygii (a group within which this particular specialization has not developed) are unrelated. 2) It also follows that any apparent similarity between the dental batteries of Dipnoi and other fishes is due to convergence rather than direct relationship.

The second major point of difference between the Dipnoi and the Crossopterygii is, of course, the nature of the skull roof. The problem resolves into two alternatives: either the dipnoan skull roof reflects an ancestral situation from which the crossopterygian condition could not have evolved, or the dipnoan condition is a specialization of the dipnoan lineage alone—in which case a dipnoan-crossopterygian relationship is not precluded. Some authors (for example, White, 1966) have considered the dipnoan skull roof pattern to be so different from that of crossopterygians as to indicate a long separation in ancestral history. Others (for example Westoll, 1949) have sought to develop schemes in which hypothetical predipnoan and precrossopterygian patterns might indicate a common ancestry of the two groups, or even the development of one pattern from another. Such schemes have been criticized recently by Jarvik (1968). It seems to us that the phylogenetic significance of a given pattern of dermal skull bones can only be understood in terms of the functional history of the whole skull. The pattern of the skull roofing bones is obviously subject to adaptive modification, like any other biological system.

All currently accepted theories concerning the development of the dermal skull pattern in vertebrates postulate the development of individual bones from a series of initial primordia around which bone is deposited. The question of "fusion" and "elimination" need not concern us here. However, it will be agreed, we believe, that regardless of the *manner* of formation of the bones, the development of any *pattern* must be controlled by, and adapted for, specific mechanical conditions. It must then follow that the dermal bone pattern in Dipnoi—essentially a mosaic with progressively larger bones toward the rear of the skull—also reflects a particular mechanical condition. Further, it seems most productive to interpret the dermal skull pattern with reference to the single most obvious feature of the cranial anatomy of Dipnoi—holostyly.

We may follow a single hypothesis with respect to the formation of dermal skull patterns: that the development of a particular pattern of dermal elements is a function of particular highly directional stresses acting in the skull as a whole. In any skull roof, where strictly oriented stresses and strains are developed due to muscular action and the relative movement of palate, braincase, and branchial arches, there seems to be a tendency for larger, specially shaped elements to occur. In the opposite case, where there are no strictly oriented forces, a mosaic of elements tends to appear. The latter is seen quite clearly in the solid snout region of many primitive vertebrates. The situation may also be modified by a separate evolutionary tendency for the number of elements in the skull roof to be diminished and for the relative size of individual elements remaining to increase, as indeed occurs in Dipnoi. The early dipnoan pattern, with a mosaic in the anterior region of the skull and in the cheek simply reflects the immobility of these regions and the underlying tissues. Probably the larger size of bones B and C in the dipnoan skull reflects the forces developed by the adductor muscles in the chamber immediately beneath these bones which are partly inserted on them. Similarly, the shape of C, B and I may be interpreted as a direct consequence of the fact that they overlay the mechanically important dorsomedian and dorsolateral cristae of the braincase. These principal characters of the dipnoan skull may be traced with small modifications (owing in part to a general decrease in ossification) throughout all lineages (see discussion of skull roof, p. 19 *ff.*, and below). The importance of their relationship to functional characteristics of the skull as a whole can scarcely be overemphasized. This type of simple mechanical analysis can be continued further and is an important tool in the interpretation of dermal bone patterns of vertebrates (Thomson, in preparation).

If the preceding is correct, then it also follows that dermal bone patterns must change as systems of cranial mechanics change. While, clearly, any given pattern must develop from a pre-existing pattern, the fact that each pattern develops ontogenetically from a mosaic condition allows modification of a pattern to proceed readily. This is particularly the case when a newly developed system of mechanics requires reversion to a mosaic rather than evolution of a new highly directional pattern of skull elements. In our estimation, therefore, all that may be inferred from the condition of the skull roof in primitive Dipnoi is that the dermal bone pattern is functionally integrated with the holostylic condition of the braincase and palate. In view of the strong likelihood that the anscestors of the Dipnoi had a hyostylic or amphistylic skull, we must conclude that, like the palate, the highly specialized condition of the skull roof in Dipnoi (as we presently know them) should not be expected to offer evidence concerning the ancestral relationships of the group. It is a product of dipnoan evolution alone.

All this is simply an affirmation of the simple and fundamental principle that continuity of structure is only possible where there is also continuity of function. In phylogenetic considerations, a discontinuity in structure is therefore not necessarily an indicator of broad phyletic separation; it may reflect a change in function within a single group. In case of the Dipnoi, a major change in cranial function has involved a complete remodeling of the skull and the "derived" dipnoan group is rather different in certain features from its sarcopterygian relatives. With respect to the lower jaw there is less difference in function and the dermal bone pattern shows closer similarities between the two groups. Once we have seen the functional basis of the unique cranial characteristics of known Dipnoi, we are able to assess their phylogenetic significance in comparison with other more conservative characteristics. Thus, we believe that the evidence of morphological similarity, for example, in the scales, cheek, lower jaw, and postcranial skeleton between early dipnoans and the Crossopterygii, is of greater significance than the more obvious differences between the two groups.

EVOLUTION OF PALAEOZOIC DIPNOI. At present, discussion of evolutionary relationships within the Dipnoi themselves must depend mainly on details of the skull roof and the dentition, though some information on the mandibles can now be added. Certain assumptions will be made in the discussion that follows, and they are now explicitly stated. Some of them follow naturally from what has been said on bone homology earlier; others depend on evidence that is not conclusive, but which seems to be reasonably safe.

1) In determining relationships between genera, the roofing bones associated with the braincase and palatoquadrate are likely to be more important than the other roofing bones.

2) Bones lost from the roof are unlikely to be regained.

3) From Early to Late Devonian, there was a common pattern of reduction of the lateral-line bones lateral to B and the posterior part of C. At first this occurred through reduction in the size of the Y, X, K, and J elements, and subsequently by loss of K and of one of the Y bones. This pattern implies a common ancestry for these forms with slight diversification of the basic holostylic cranial mechanism.

4) The shape and number of the fins are unlikely to be of greater significance for understanding evolutionary relationships than the structure of the roofing bones of the skull. There is too great a possibility for convergent or parallel evolution in fin structure in accordance with particular modes of swimming (see Thomson, 1969).

5) The character of the teeth is clearly related to mode of feeding. There seems to be no inherent reason why animals of a single stock should not diversify their feeding habits and therefore their dentition. This could involve either the gain or loss of denticles or of a tooth pattern. Given our present knowledge of the Dipnoi, the nature of the dentition alone is not necessarily a reliable guide to phylogenetic relationship (cf. Denison, 1968a, p. 386). This point can also be demonstrated empirically by appeal to *Uranolophus* and *Dipnorhynchus*. These are the earliest known dipnoan genera, and have skull shapes, dermal roofing bone and mandibular dermal bone patterns, palatal structures, anterior mandibular furrows, and Meckelian vacuities so similar that it would be difficult to deny that they are closely related. Yet they have very different dentitions.

6) The size and shape of the mandible and its muscle insertion areas will also be related to method of feeding and should not be used in preference to dermal bone patterns to indicate relationships.

7) The form of the parasphenoid, being the base of the braincase, is likely to be important.

In the following discussion of the general course of dipnoan evolution, we are obviously unable to document precisely the origin and relationships of particular known fossil genera. However, the citing of these genera offers the only convenient means of indicating the relationships of the lineages of which we believe they formed a part.

The Early Devonian genera *Uranolophus* and *Dipnorhynchus* are at a similar level of development in numerous characters—the multiplicity of roofing bones anterior to D; the large size of X and K; the small size of L; the junction of the I bones behind B; the extension of the supra-orbital canal from K into J; the presence of at least two O bones; the lack of a junction between the canals in X and K; the long cheek; the lack of a parasphenoidal stalk; large lower jaw; well-ossified Meckelian cartilage; similarly arranged dermal bones and lateral-line canals in the lower jaw. All these characters may fairly be regarded as primitive. However, *Uranolophus* is distinct in having large E bones that are in contact with C; a fairly large D; no pineal foramen; a marginal tooth row and denticulate palate and prearticular. The evidence is not strong one way or the other, but the character of the D and E bones suggest that *Dipterus* was derived from a *Uranolophus*-like rather than a *Dipnorhynchus*-like form despite the fact that the former is older. This is interesting in view of the freshwater habitat of *Dipterus* and *Uranolophus.*

The transition from *Uranolophus* to *Dipterus* involves the reduction in size of K and X as the eye moves back and the cheek shortens; the parting of the I bones behind B; the reduction of the number of bones in the snout; the reduction of the number of O bones to one; the increase in size of the L and M elements; the junction of the infra- and supra-orbital canals between K and X; the capture of the occipital commissure by I and the loss of H; the development of ceratodont dentition and a parasphenoidal stalk; the close approach of the oral and mandibular canals with a modification of the angular-surangular relationships; and the reduction of the Meckelian vacuity.

From *"Dipterus,"* three stocks radiate into the Upper Devonian—one to *Scaumenacia* and *Phaneropleuron;* a second to *Fleurantia, Soederberghia, Oervigia* and *Jarvikia;* and a third to *Rhinodipterus secans.* In view of the fact that certain of the genera grouped together here have previously been considered to be in different groups (e.g., *Phaneropleuron* and *Scaumenacia* are placed in different Orders by Lehman, 1959, by virtue of their different fin arrangement) some justification of this phylogeny is necessary. The similarity of the skull roof in *Scaumenacia* and *Phaneropleuron* has been noted by several authors (Westoll, 1949). In both, the bones B, C, and E are greatly enlarged, but D is lost; K has disappeared from most specimens of *Scaumenacia* and many specimens of *Phaneropleuron;* and both have ceratodont dentition. The main differences are in the relatively larger size of L and the development of a single dorsocaudal fin in *Phaneropleuron.* Both these differences can be easily accounted for by evolution along established dipnoan trends, *Phaneropleuron* being the younger form. The presence of K in a higher proportion of specimens of *Phaneropleuron* than *Scaumenacia* suggests that they are not on the same line of descent. Little is known of the late Givetian genus *Pentlandia,* but there is no reason at present to doubt the view of Watson and Day (1916) that it is closely related to *Scaumenacia.*

The *Fleurantia* stock is characterized by an elongate head, the loss of K and D, the occasional complication of C, the enormously long L and E and the very long parasphenoid with a bifid termination of its posterior stalk. *Soederberghia* is probably the end product of an early offshoot from this stock. It retains the lateral-line canal (rather than a pit line) from X to J and it has a pair of bones on the infra-orbital lateral line below X occupying the position of 4, but neither of them is in contact with the orbit. These features are not known in any other dipnoan. All its other characteristics, except its almost smooth palate, ally it with the *Fleurantia* stock. It is possible that the main part of the stock developed through *Rhinodipterus ulrichi.* (For a discussion of *R. ulrichi* and *R. secans,* see p. 37).

The third main stock is represented by *Rhinodipterus secans.* This has retained many of the characters of *Dipterus* that are lost, or partly lost, in the other two, e.g., bones D, O, and K and the continuation of the lateral-line canal from K to J. On the other hand it has a posteriorly projecting I and a long posterior parasphenoidal stalk, differentiating it from *Dipterus.* The only known material occurs in the lower Famennian and is thus coeval with *Fleurantia* and *Scaumenacia.* The importance of this stock is that it provides the only possible origin for the Early Carboniferous and later genera (all of which retain D) unless one is prepared to admit the possibility of the redevelopment of a bone in the D position in the *Scaumenacia* stock. This we do not accept.

Two stocks are present in the Lower Carboniferous—the *Ctenodus* stock and the *Sagenodus* stock. The former is characterized by relatively large paired C and E with a smaller D at the angle of junction of these four bones. In the latter stock C has atrophied and the vacated space is occupied by a forward extension of B and an enlargement of D. Both exhibit a number of features absent from all Devonian forms: with the doubtful exception of *Conchopoma* all genera show the capture of the occipital cross commissure by B and the incorporation of Z in the skull table. The parasphenoid, in all genera in which it has been observed, namely *Sagenodus, Conchopoma, Uronemus,* and *Ctenodus,* has a flatter rather massive anterior rhombic portion that lacks a continuation of the groove present on the

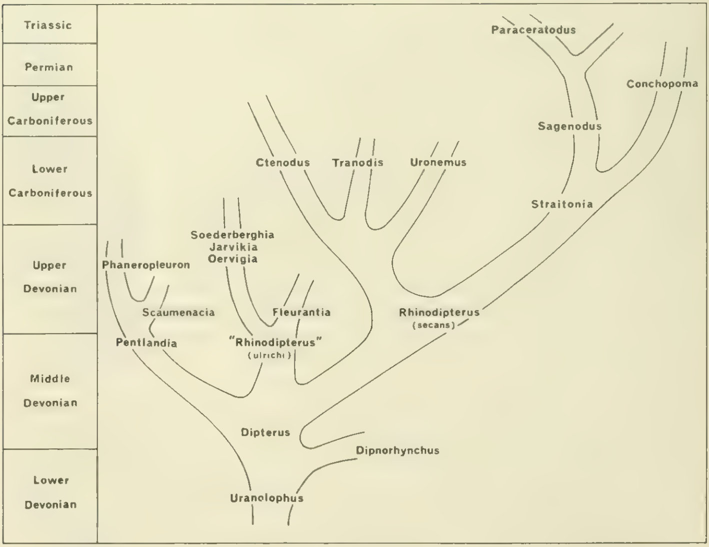

Triassic
Permian
Upper Carboniferous
Lower Carboniferous
Upper Devonian
Middle Devonian
Lower Devonian
Paraceratodus
Conchopoma
Sagenodus
Ctenodus
Tranodis
Uronemus
Straitonia
Soederberghia
Jarvikia
Oervigia
Phaneropleuron
Scaumenacia
Fleurantia
Rhinodipterus
(secans)
Pentlandia
"Rhinodipterus"
(ulrichi)
Dipterus
Dipnorhynchus
Uranolophus

FIG. 35. Phyletic relations of known Paleozoic Dipnoi in the light of the present discussions.

ventral surface of the posterior stalk. In addition, the termination of the parasphenoidal stalk, at least in *Sagenodus* and *Ctenodus,* is rounded rather than bifid. These features suggest that the two stocks had a common origin during the Late Devonian or perhaps the Early Carboniferous, and that they have adopted basically different means of reducing the number of roofing bones. Within each stock the dentition shows a wide range of variation. *Sagenodus, Ctenodus* and *Tranodis* are ceratodont; but *Uronemus* and *Conchopoma* have a large number of small teeth covering the palate, and in addition *Uronemus* has a row of compressed marginal teeth. Some workers have thought that *Uronemus* and *Conchopoma* are probably related because of their similar dentition. However, in *Uronemus* the biting surfaces are apparently restricted to the pterygoids while in *Conchopoma* the pterygoids are very narrow and the enlarged parasphenoid carries most of the denticles, suggesting that the two genera represent entirely separate adaptations to the same mode of feeding.

The main line of development to the Mesozoic *Ceratodus* was through the *Sagenodus* stock. Carlson (1968) has already argued cogently in favor of this view using roofing-bone data similar to ours.

This evolutionary scheme (Fig. 35) is different in many respects from those recently proposed by various authors, and it has certain important taxonomic implications. Bertmar (1969) has attempted to construct a phylogeny of the Dipnoi. His discussion lacks detail and depends in part on questionable evidence such as the presence of maxillaries and premaxillaries in certain Devonian genera; the use of a longer snout to indicate relationships in the absence of data on the skull structure in others; and the use of the structure of the endocranium to trace the lineages of the Ceratodontidae and Lepidosirenidae back to *Chirodipterus,* when in fact the roof of *Chirodipterus* is unknown and hitherto its endocranium has been the only Paleozoic one that has been reasonably well known. As might be expected from what has already been indicated, there is little agreement with the classification of Lehman (1966) which, at the ordinal level, is based entirely on fin arrangement. There is a measure of agreement with the scheme proposed by Vorobjeva and Obruchev (1964, fig. 17), but the differences between our interpretations of the Carboniferous and Permian forms are great. These authors have attempted to use a wide range of characters in the definition of the major taxa, e g, the degree of ossification of the endocranium, the structure of the dermal bones and scales, nature of the dentition and fins, as well as cranial roofing bone and mandibular dermal bone patterns. However, these characters are not consistently applied, mainly because of the inadequate preservation of many genera. Consequently many of the taxa seem to have arbitrary limits, and a large number of assignments of genera are acknowledged to be doubtful. One may take as an example the differences between their definitions of the suborders *Uronemoidei* and *Ctenodontoidei;* although "paired lateral occipitals" are listed for the *Uromemoidei* but not the *Ctenodontoidei,* and only the postsplenial and angular in the former and the postsplenial, splenial, and angular in the latter, are said to be fused, we can find no evidence to support discrimination on these bases (Watson and Gill, 1923; Westoll, 1949). The remaining differences listed refer to the degree of ossification of the endocranium and axial skeleton, the depth of burial of the lateral-line canals, and the dentition. These provide inadequate grounds for division at the subordinal level unless reinforced by strong phylogenetic arguments; such are not available.

Other problems arise, such as the separation of *Soederberghia* and *Fleurantia* into different families, but these are relatively minor.

Excluding those genera for which inadequate skull roofs are available, it can be seen that the classification of Romer (1966) produces groupings very similar to those outlined in our Figure 35. There are differences, as, for example, in the treatment of *Rhinodipterus* and *Pentlandia* and the relative status assigned to certain groups. The problem of *Rhinodipterus* has been discussed previously and need not detain us further. *Pentlandia* is, in our view, more closely allied to *Scaumenacia* than to *Dipterus,* and in Romer's classification should be assigned to the Phaneropleuridae. Finally, if the Uronemidae are to be separated from the Ctenodidae, and the Conchopomatidae from the Sagenodidae, as Romer suggests, the group *Phaneropleuron-Scaumenacia-Pentlandia* should be separated from that containing *Soederberghia-Jarvikia-Oervigia-Fleurantia-Rhinodipterus ulrichi,* even if subdivision of these groups is not carried further.

SUMMARY

Dipnorhynchus sussmilchi is shown to be an early Emsian-early Eifelian marine-dwelling dipnoan, adapted to feeding on shelly invertebrates or perhaps dead placoderms. Preparation of new material and of the holotype has shown that previous reconstructions have been in error because of the misinterpretation of the position of the infraorbital lateral-line canal and the consequent positioning of the orbit too far forward. A new reconstruction of the skull roof is given.

Using this reconstruction as a basis, and accepting the postulates that space capture rather than fusion offer the best basis for interpreting the dipnoan skull roof and that the bones on the posteromedian part of the skull provide the most stable points of reference, a series of definitions for the roofing bones is developed and applied to a representative series of Devonian and late Paleozoic genera. New features found in the roof of *Dipnorhynchus sussmilchi* are the complex division of the lateral-line system behind the orbit where there is a bone, T, not present in later genera; the complex D elements and the paired O elements; the probable existence of an H element between A and Z; the position of the occipital commissure on the loosely articulated elements Z-H-A; the absence of a rostral commissure; and the support of I by the dorsolateral crista of the braincase and of Y by the palatoquadrate.

The discovery of an isolated cheek plate carrying the lateral line canal and the determination of the position of the operculum from its attachment to the palatoquadrate have permitted the reconstruction of the cheek region, which is longer than that of all other known genera except *Uranolophus*. It is also more complex and contains many more bones.

The mandible of *D. sussmilchi* is a massive structure. The dermal bones can be readily compared with those of *Dipterus*. There is a long surangular extending from the articulation to the dentary, and similarly elongate angular, postsplenial and splenial. The prearticular is very robust and carries dental surfaces complementary to those of the palate. The dentary is well ossified and its dorsal surface extends back to make a long narrow dental ridge similar to a colinear ridge on the prearticular. In the curve of the dentary is a deep anterior furrow that may have contained sensory tissue in life. A large labial pit is present. The Meckelian bone is thick and strong and provides a surface for the attachment of the intermandibularis and geniocoracoideus muscles. It also forms a symphysial plate. Both mandibular and oral lateral-line canals are present, together with a mandibular commissure. The oral canal seems to terminate posteriorly within the surangular. Within the dentary there is a system of rostral tubuli of the same type as in the snout. A system of nerve and vascular canals can be readily distinguished and has been compared with those of *Neoceratodus*. Despite the obvious differences in size and dentition, and the length of the surangular, the basic structure of the mandible is shown to be essentially the same as that of *Dipterus*.

The palate of *D. sussmilchi* is a massive structure, lacking separate denticles and sutural indications of a separate parasphenoid element. The dental surface is marked by a series of massive rounded tuberosities that cannot be homologized with any structures in other Dipnoi. The palate is fused to the braincase without any indication of the original boundary between endocranial, palatal, and dermal components of the holostylic skull. The braincase is similarly fused to the dermal skull roof. The nasal capsules are large and the nares ventrally directed. The nasal organ was apparently subdivided into three separate recesses. The orbital and temporal chambers of the skull are delimited and partially separated by a curious dorsal process from the palate found elsewhere only in *Uranolophus*. The oticotemporal region of the braincase is covered laterally by the apposed massive palatoquadrate, forming an enclosed chamber around the trigeminofacialis nerve ganglion complex. Posterodorsally there is a massive adductor muscle chamber extending backward under the skull roof. Each chamber is subdivided by a dorsolateral crista of the braincase that rises to meet the underside of the skull roof; the chambers on either side are separated by a similar median crista. A similar arrangement is seen in *Chirodipterus* and *Dipterus* and the large adductor chamber is a common feature of all known Dipnoi.

A unique feature of the braincase of *D. sussmilchi* is that it included a unique otoquadrate bar, possibly homologous with the hyomandibula. In front of this is a deep recess, probably for a spiracular sense organ.

The scales and the fine structure of the dermal bones of *D. sussmilchi* are almost identical with those of *Uranolophus* and show marked similarity to those of Crossopterygii.

A new outline scheme for the evolution of the Paleozoic Dipnoi is presented. It depends primarily on dermal bone patterns of the head, but also takes into account such structures as the parasphenoid and the fins. It is our opinion that the new data on the hyomandibula, the cheek, the dermal bones of the mandible, and the scales provide strong evidence for the close relationship of the dipnoans and crossopterygians, and for the sarcopterygian concept of Romer.

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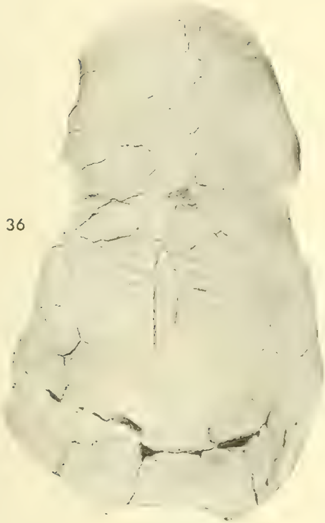
FIGURES 36–95

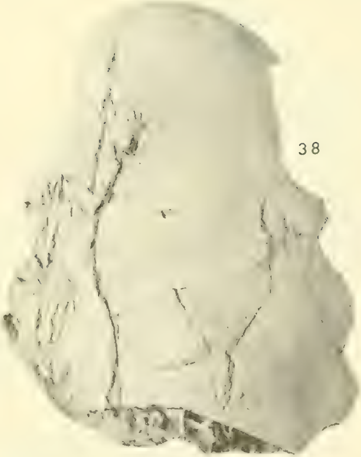
Figs. 36–39. The skull of *Dipnorhynchus sussmilchi.*

36. Specimen 18815, Australian National University. Dorsal view. ×.77.
37. Anterior view of same specimen as Figure 36. × .95.
38. Holotype. Dorsal view. ×.77.
39. Anterior view of same specimen as Figure 38. ×.95.

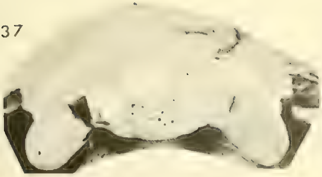
36



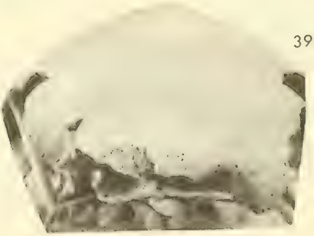
38



37

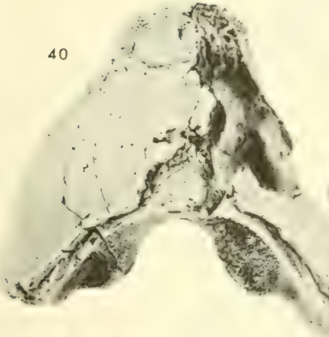


39



Figs. 40–45. *Dipnorhynchus sussmilchi.* Mandible, specimen P 46773, British Museum (Natural History).

40. Mandibles in ventral view. ×1.0.
41. Mandibles in dorsal view. ×1.0.
42. View toward the anterior along the Meckelian vacuity of the right ramus, prearticular and Meckelian bone on the left, postsplenial and part of the articular at the bottom. Note the furrows across the latter bones, the left one leading to the foramen in the anterior furrow and the right to a foramen opening into the rostral tubuli. ×1.5.
43. Posteroventral view of mandibles. ×1.0.
44. Right mandible in lateral view. ×1.0.
45. Left mandible in lateral (and slightly anterior) view. ×1.0.



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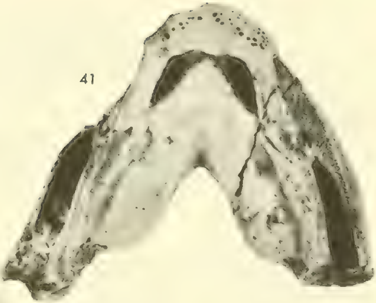

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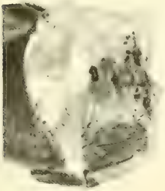

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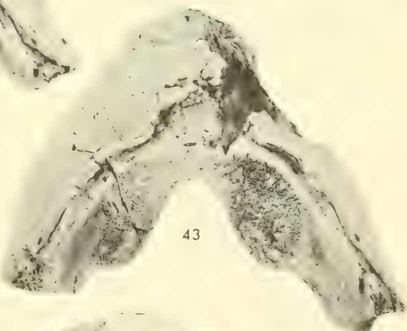

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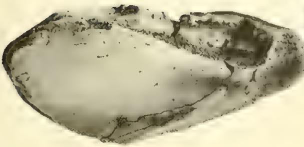

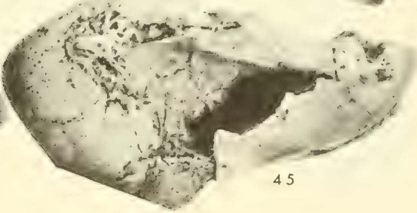

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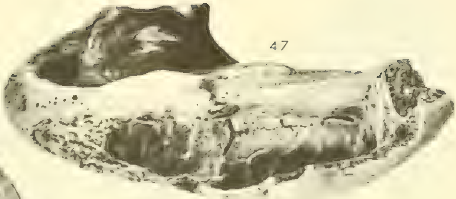
Figs. 46–50. *Dipnorhynchus sussmilchi.* Mandible. Figs. 46–47, same specimen as Figs. 40–45. Figs. 48–50, specimen P 13837, National Museum, Melbourne.

46. Mandible in dorsal view. ×0.75. (Specimen, not whitened, showing well the deep median groove.)
47. Left mandible in lateral (and slightly dorsal) view, showing the Meckelian vacuity. ×1.1.
48. Left mandible in lateral view showing the vertical ridges in the medial wall of the Meckelian vacuity. ×0.85.
49. Right mandible in ventral view, showing the Meckelian vacuity. ×0.85.
50. Mandibles in dorsal view. ×0.75.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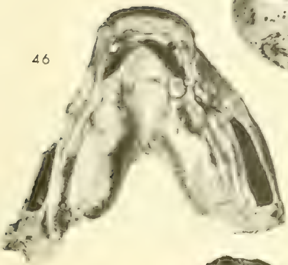
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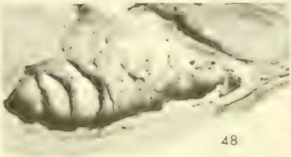
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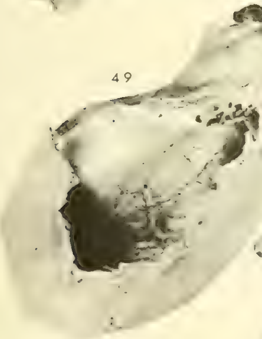
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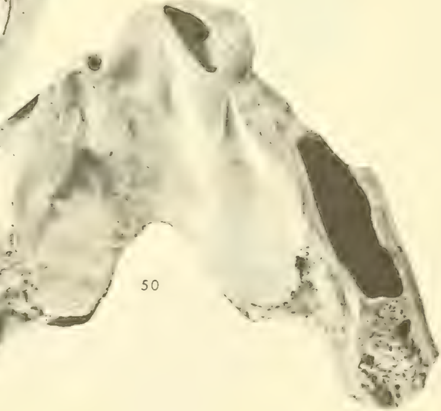
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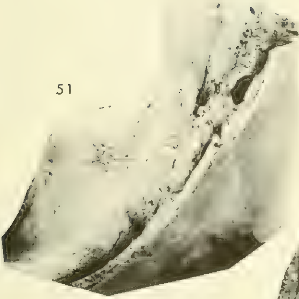
Figs. 51–54. *Dipnorhynchus sussmilchi.* Mandible, same specimen as in Figs. 48–50.

51. Posteroventral view of posterior end of right ramus. ×0.9.
52. Ventral view of right ramus. ×0.9.
53. Posterior view of mandibles. ×0.75.
54. Anterior view of mandibles. ×0.75.

51



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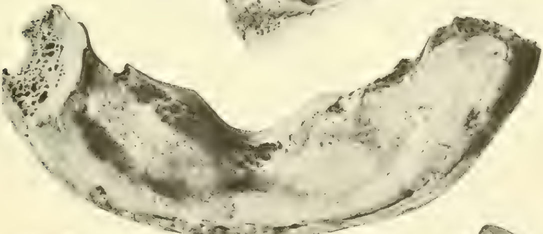

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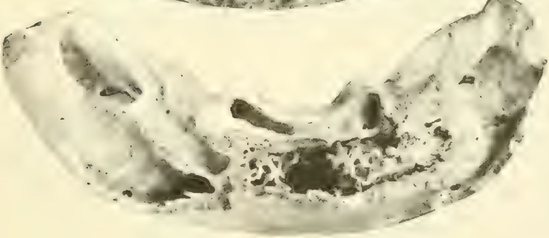
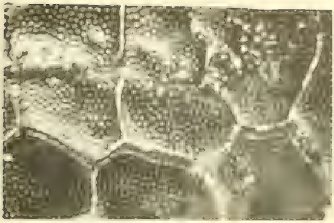


Figs. 55–62. *Dipnorhynchus sussmilchi.*

55. Detail of dermal bone surface in rostral region. Specimen 18815, Australian National University. ×5.5.
56. Detail of bone structure on the upper posterior surface of the dentary. Photographed under alcohol. Specimen P 33714, British Museum (Natural History). ×42.
57. Detail of bone structure on rostral part of dentary; large pores open into rostral tubuli. Photographed under alcohol. Same specimen as Fig. 56. ×21.
58. Detail of surface of postsplenial showing cosmine. Surface oiled. Same specimen as Fig. 56. ×21.
59. Detail of surface of right surangular. Specimen P 33714, British Museum (Natural History). ×1.4.
60. Detail of posterior end of right mandibular ramus. Posteroventral view. Same specimen as Fig. 59. ×1.4.
61. Detail of dorsal surface, posterior end of right jaw ramus. Same specimen as Figs. 59 and 60. ×1.4.
62. Ventrolateral view of broken edge of left dentary showing the rostral tubuli, the ragged edge of the enamel surface of the dentary overlapping the spongy bone of the inner wall of the labial pit, and the canal system on the medial wall of the Meckelian vacuity. Specimen P 46773, British Museum (Natural History). ×1.4.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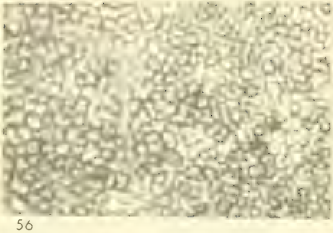
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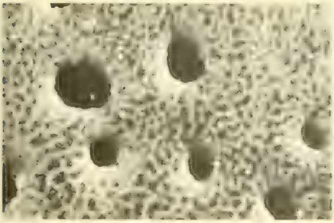
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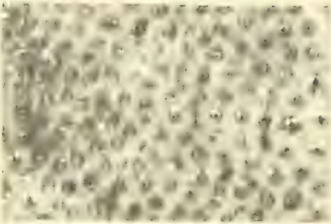
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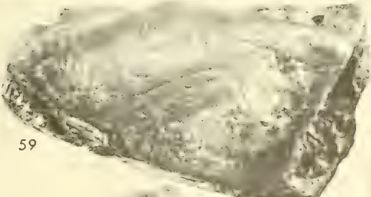
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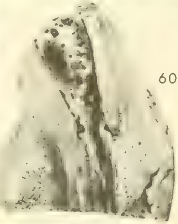
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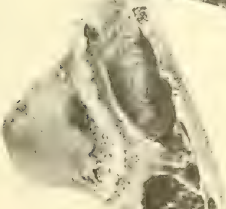
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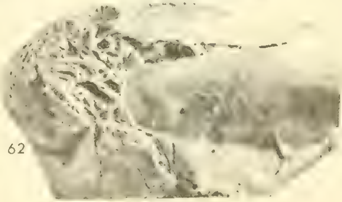
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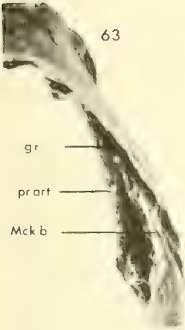
Figs. 63–68. *Dipterus valenciennesi.* Mandible, specimen 53377, Geological Survey, London (Figs. 63–67). Palate, specimen 1859.33.612, Royal Scottish Museum, Edinburgh (Fig. 68).

63. Ventromedial view of left mandibular ramus. ×1.5.
64. Ventral view of mandibles. ×1.1.
65. Ventral view of left ramus. ×1.5.
66. Lateral view of left ramus. ×1.5.
67. Cross section through right mandibular ramus, seen in anterior view. ×3.0.
68. Palate, incomplete; ventral-surfaced solum nasi eroded showing vascular canals within. ×0.75.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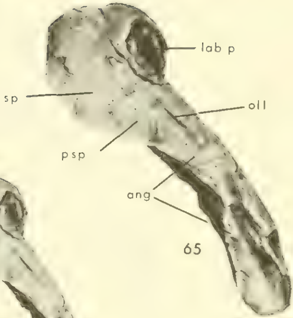
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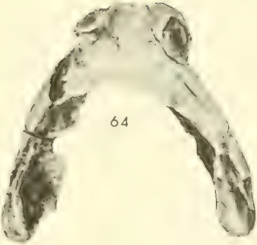
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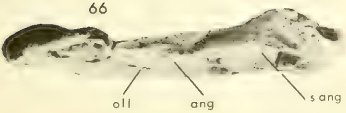
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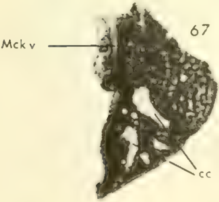
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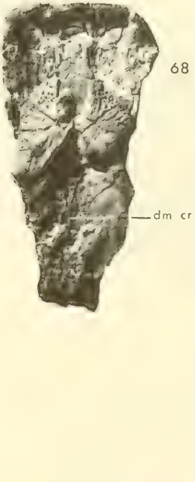
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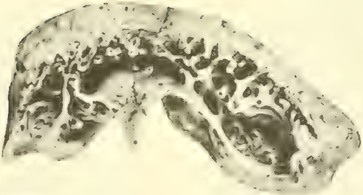
Figs. 69–73. *Dipnorhynchus sussmilchi*. Palate. Specimen 33699, British Museum (Natural History).

69. Detail of portion of snout region broken through naturally, showing the rostral tubuli. Dorsal view. ×0.95.
70. and 71. Portion of the snout and incomplete palate, in ventral view. Natural association. ×0.8.
72. and 73. Portion of the snout and incomplete palate, in dorsal view. Natural association. ×0.8.



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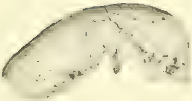

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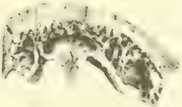

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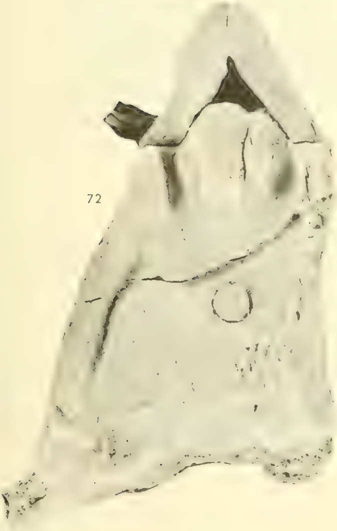

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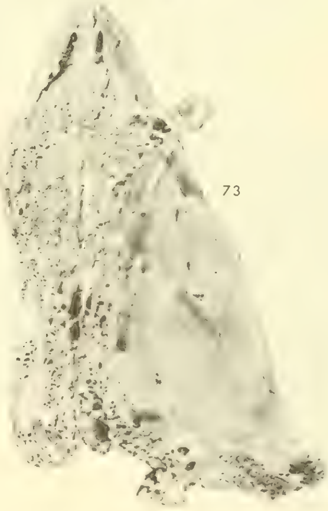

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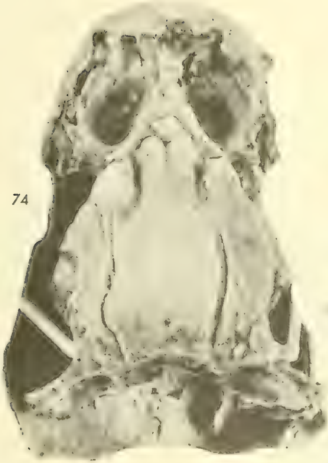
Figs. 74–77. *Dipnorhynchus sussmilchi.* Braincase and palate.

74. Ventral view of skull. Specimen 18815, Australian National University. ×0.8.
75. Ventral view of skull. Holotype. ×0.8.
76. Posterior view of skull, same specimen as Fig. 74. ×0.85.
77. Detail of quadrate region of the palate. Same specimen as Fig. 75. ×1.1.

74



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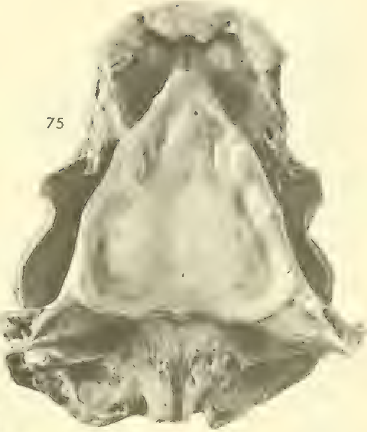

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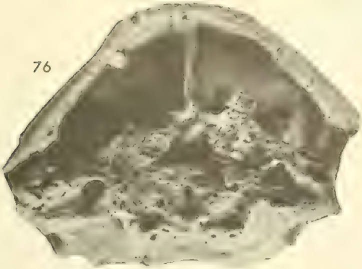

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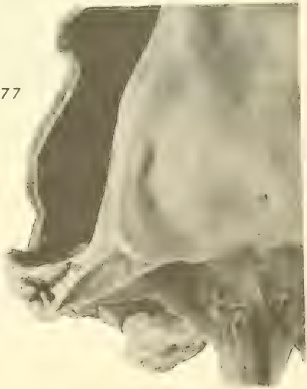

Figs. 78–81. *Dipnorhynchus sussmilchi.* Skull and lower jaws.

78. Skull in right ventrolateral view, showing lateral wall of braincase. ×0.75.
79. Anterior portion of skull in left lateral view showing the small rounded irregular tubercles along the palate margin. Specimen 18815, Australian National University. ×0.8.
80. Mandibles in lateral (and slightly dorsal) view. Specimen P 46773, British Museum (Natural History). ×1.1.
81. Skull in right lateral view, showing ventral portion of lateral wall of braincase. Same specimen as Fig. 78. ×0.75.

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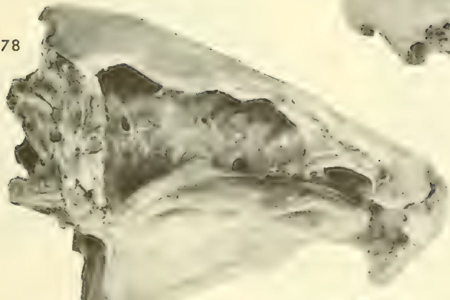

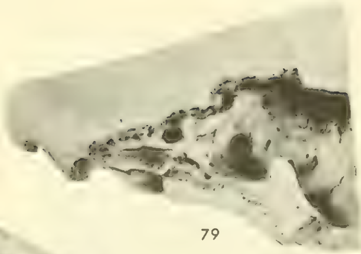

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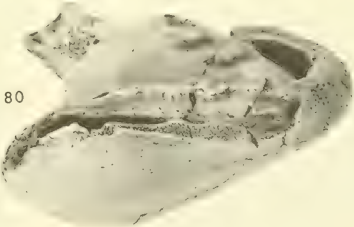

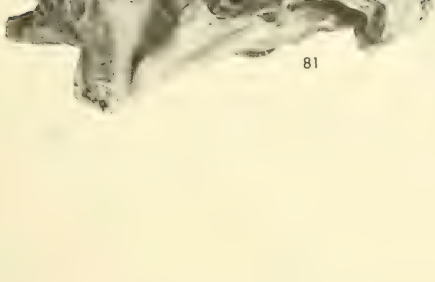

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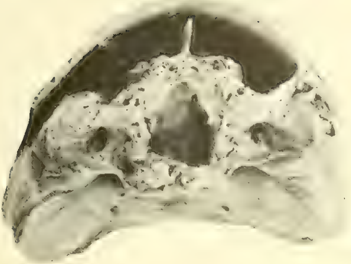
Figs. 82–85. *Dipnorhynchus sussmilchi.* Braincase.

82. Posterior view of braincase. Holotype. ×0.7.
83. Detail of the region of the jugular canal. Holotype, same posterior view as Fig. 82. ×1.1.
84. Posteroventral view of posterior region of the skull. Holotype. ×0.7.
85. Posteroventral view of the posterior region of specimen 18815, Australian National University. ×0.8.

82



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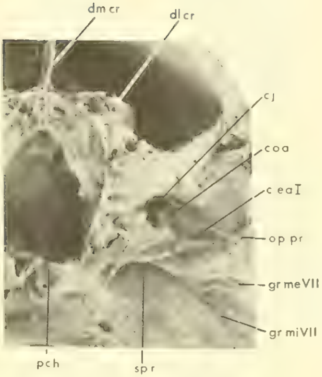
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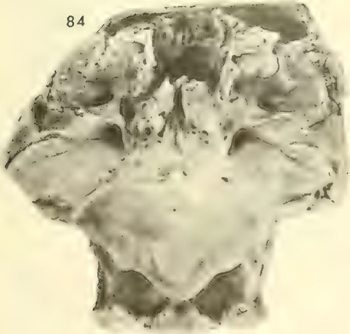

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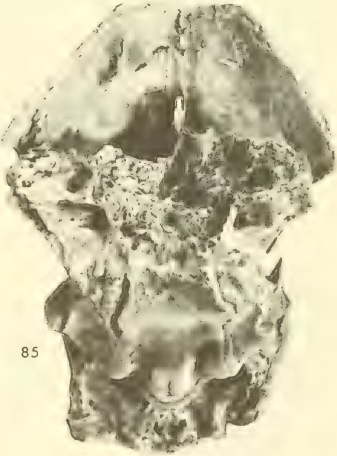

Figs. 86–91. *Dipnorhynchus sussmilchi.* Scales, branchial element and cheek element.

86. Scale in (a) lateral and (b) medial view. P 13837B, National Museum, Melbourne. ×1.6.
87. Two scales in medial view.
    (a) P 13837C, National Museum, Melbourne. ×1.6.
    (b) P 13837F, National Museum, Melbourne. ×1.6.
88. Scale in (a) lateral and (b) medial view. P 13837D, National Museum, Melbourne. ×1.6.
89. Scale in (a) lateral and (b) medial view. Portion of Holotype (F 10813B), Australian Museum, Sydney. This was originally described as part of the palatal ornamentation; see text. ×1.6.
90. Portion of hypobranchial skeleton in (a) ventral, (b) right lateral, and (c) dorsal view. P 13837G, National Museum, Melbourne. ×1.6.
91. Isolated element 8 from right cheek in (a) posterior, (b) lateral, and (c) medial view. Specimen P 13837A, National Museum, Melbourne. ×1.2.

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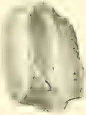

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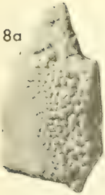

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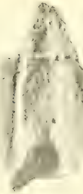

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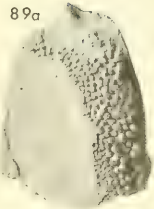

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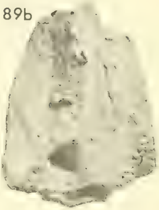

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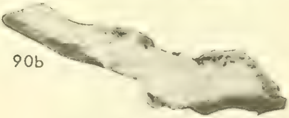

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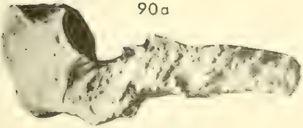

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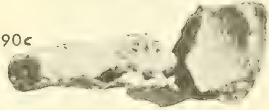

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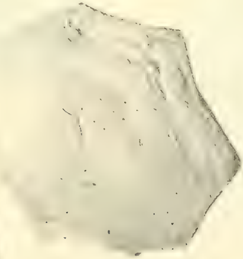

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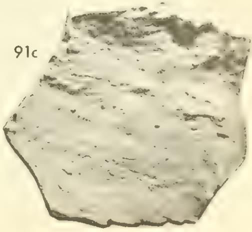

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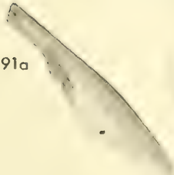

Figs. 92–95. *Dipnorhynchus sussmilchi*. Mandibles, palate, and cheek.

92. Mandibles in ventrolateral (and slightly posterior) view as seen by X ray. The X-ray beam is perpendicular to the axis of the left mandibular ramus. Specimen P 46773, British Museum (Natural History). ×0.8.
93. Mandibles in ventral view, as seen in X ray. Same specimen as Fig. 92. ×0.8.
94. Palate in dorsal view, as seen in X ray. Specimen P 33699, British Museum (Natural History). ×0.8.
95. Element 8 from right cheek, as seen in X ray. Specimen P 13837A, National Museum, Melbourne. ×0.8.

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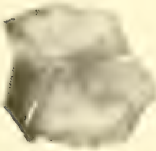

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